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DISCOVERY OF THE DISK OF ONYCHOCRINUS, AND FURTHER REMARKS ON THE CRINOIDEA FLEXIBILIA

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The Disk of Onychocrinus

In the year 1888 Wachsmuth and Springer[1] published their "Discovery of the Ventral Structure of *Taxocrinus*," based upon a remarkable specimen of *T. intermedius* from the Kinderhook group of the Subcarboniferous, at Le Grand, Iowa. Until that time nothing whatever had been known concerning the structure of the tegmen in the Crinoidea Flexibilia; but numerous theories about it had been discussed, all of them based upon the assumption that it was in the nature of a closed vault analogous to that of the Camerata, and supposed to be common to all the paleozoic Crinoids. The specimen above mentioned, however, demonstrated that in *Taxocrinus*, and presumably in the Flexibilia generally, the tegmen had an open mouth, surrounded by five oral plates, with ambulacra passing in between them, after the manner of the Recent Crinoids. This interpretation has been accepted by all subsequent writers, and our figure of the tegmen of *Taxocrinus* has been copied in almost every treatise on Crinoids or general paleontology published since that time.

In that paper it was stated that traces of alternating ambulacral plates had been seen in a specimen of *Onychocrinus*, but not the orals,

[1] *Proceedings*, Academy of Natural Science, Philadelphia, November, 1888, p. 337.

nor any part of the perisome. Messrs. Lyon and Casseday, in their description of *Onychocrinus exsculptus*,[1] gave a partial description of the vault, which they thought to be similar to that of the Asteroidea. They observed, extending toward the arms, "five rays composed of two rows of large, granulose pieces, one row alternating with the other," and in the fields bordered by these five rays some interstitial pieces which were "very small, granulose, and arranged without any apparent order." They were unable, from the fragmentary condition of their specimens, to obtain any information as to the central portion.

As the genus *Onychocrinus* represents the most specialized form of the group—one of the latest developed and latest surviving—it has seemed a matter of special interest to ascertain the exact structure of its ventral side. Its calyx exhibits, in a striking degree, the two characteristics of the group—massiveness and flexibility. Except at the very base, where they are rather thin, the plates are thick and heavy, and are closely laid together, like bricks in a pavement. The interbrachial system connecting the rays dorsally is composed of strong and thick plates, while the brachials are of great depth, and have a very shallow ambulacral groove. Nevertheless, the plates of this powerfully built calyx must have possessed an immense amount of mobility among themselves, for we find it preserved in a great variety of positions. In some specimens the rays are folded together, and in others they are spread out horizontally. These changes of position, while they involve all the brachial and interbrachial plates, did not cause any marked opening or gaping of the sutures; but in some singularly perfect manner the plates seem to have been capable of sliding upon each other by their apposed surfaces, and thus accommodating themselves to any degree of flexure.

The tegmen of such a calyx must necessarily have been of an extremely pliant nature. But all attempts to obtain it, in sufficiently perfect condition to disclose the nature of the mouth and oral structures generally, have hitherto proved futile. At Crawfordsville, Ind., where two species have been found in large numbers, the specimens almost always have the rays so closely folded together that the tegmen cannot be got at, and, besides, the preservation of fine details

[1] *American Journal of Science*, (2), Vol. XXIX, p. 79.

at that locality is poor. At Burlington specimens of this genus have not been found in a matrix soft enough to permit the exposure of such delicate structures. At Le Grand, where the *Taxocrinus* disk was found, *Onychocrinus* does not occur—not having been developed in America, so far as yet known, earlier than the Upper Burlington Limestone.

The only known material which seemed to offer a possibility of discovering the tegmen of this genus was that from Indian Creek, Montgomery County, Ind., where *Onychocrinus ulrichi* was obtained in considerable numbers; many of them with the rays completely spread out horizontally, and imbedded in a fine-grained, homogeneous matrix, admitting of minute cleaning. In collecting, these were usually found with the dorsal side exposed and the ventral side embedded, and when the collection was first made from that locality, several such specimens were cleaned without yielding the desired result. Remnants of the disk were observed in some, broken and lying in confusion in the bottom of the cavity, and showing but little of the structure. It was clear that the disk was of such extreme flexibility that it had been forced by the pressure of the calcareous matrix down into the dorsal cavity, and was generally broken and displaced. Recently I undertook the search afresh, and by very delicate manipulation had over a dozen of the best specimens with outspread rays completely freed from the matrix on the ventral side—a very tedious and laborious operation, and sometimes sadly destructive of fine specimens. Some were dissected by the removal of the calyx plates, in hope of gaining access to the under side of the disk.

These efforts were finally rewarded by uncovering, in several specimens, the tegmen in such position as to give a complete elucidation of the structure. The exceptional condition of the specimens, and the exceedingly fine and homogeneous character of the material in which they were imbedded, were all that rendered the discovery of these details possible. With the light afforded by them several others in which the structures were only partially preserved—though much displaced—became easily understood. The construction of this disk is upon the same general plan as that of *Taxocrinus*, but exhibits a very interesting modification of it. It is gratifying to find, in this new discovery upon an additional genus, a full confirmation

of our former interpretation of the tegmen of the whole Flexibilia group.

The two most instructive specimens are figured herewith (Plate IV, Figs. 1 and 2), and another which gives a good general idea of the disk (Plate IV, Fig. 3). Fig. 1 will be readily understood by the simple statement that it is the ventral surface of the disk. In Fig. 2 we see the inner floor, or under side of the same structure, which has been exposed by removing the basal, radial, brachial, and interbrachial plates. The disk is so pliant and frail that it is invariably found more or less sunken down, and lying on the bottom of the dorsal cavity. This is why it appears concave in Fig. 1, and convex in Fig. 2. The greater portion of the disk was clearly membranous, with calcareous spicules and granules imbedded in it; except in the oral center, and in the ambulacral regions, which are occupied by rows of large elongate, alternating plates, more or less tumid exteriorly, and keeled on the under surface. These converge in the middle into a rounded, open mouth, which is surrounded by a pyramid of four small, triangular oral plates, meeting a fifth large one on the posterior side. This posterior oral is the most remarkable feature of the disk. It is of enormous size relatively to the other structures, and is very thick and heavy. It is preserved in nearly all the specimens in which the ventral side was cleaned, but as it was usually found lying detached in the bottom of the dorsal cavity, its identity was not recognized until after I found it in place in this specimen (Fig. 1). It is spade-shaped, and the end toward the oral aperture is somewhat hollowed to form one side of the mouth. Both the exterior and interior surfaces of this large plate are shown in the figures—the latter view being at the upper part of Fig. 2. In Fig. 1 this plate seems to be divided by a transverse suture, but I do not find this to be so in other specimens.

The four smaller oral plates are delicate, and they seem to vary somewhat in shape in the different specimens—sometimes appearing quite slender and elongate, and irregular in size. Much of this irregularity, however, may be due to the accidents of fossilization, producing such compression and displacement as might greatly modify the shape and proportions of these delicate structures. In the specimen represented by Fig. 1, two of these plates are perfect and undisturbed, the third somewhat flattened laterally, and the

fourth is pushed partly under the others, so that not much of it can be seen in this view. They are triangular, and fit closely together at the sides, forming a small pyramid. As they lie in the bottom of the calyx they seem to stand somewhat erect, but in their natural position, with the disk normally distended, it is probable that they would appear more flattened, like the orals in the recent genus *Holopus* (Plate V, Fig. 8). They were perhaps also movable, capable of opening and closing at the will of the animal. These small orals are not always so regular as this. Fig. 4, Plate IV, which is an enlarged view of the central part of the disk in another specimen, shows the irregular, elongate, toothlike appearance which they sometimes present. The rounded object at the right of the three linear plates is evidently a foreign body, but the other four suggest a stage of almost complete resorption.

The ambulacra are composed of relatively heavy, elongate plates. They meet by close sutures, and are convex on the outer surface. The inner surface is marked by keel-like elevations, which may have served as lines for muscular attachment. They extend from the oral center along the rays to the point of bifurcation, beyond which they have not been traced; but they no doubt follow the arms in a modified form. The three anterior ambulacra pass in between the bases of the four small orals in a similar manner as they do between the plates of the oral pyramid in *Holopus*. The two posterior ambulacra first meet the outer corners of the large oral—at which points there are some larger plates, apparently serving as braces, or supports, for the tegmen—thence they run along the edges of the posterior oral, which sometimes appears to be grooved, and pass in toward the mouth at the junction between it and the smaller orals. Whether these strong alternating plates were covering pieces arching over the food-grooves, or were merely some kind of subambulacral plates forming a support for more delicate plates which were not preserved, or for an ambulacral structure composed only of soft parts, I am unable to determine. The variation in size and shape of ambulacrals in the living Crinoids is very great, and there is no reason why plates as large as these may not have served as covering pieces, opening out when the orals did to admit the inward passage of the food-bearing currents.

The connecting integument between the ambulacra was mem-

branous, reinforced by a close growth of calcareous particles similar to what has been observed in *Taxocrinus*, *Uintacrinus*, and the disk of many Recent Crinoids. It extends far out along the rays, bordering the ambulacra as far as they have been traced. It is extremely frail in the fossil, and is of a slightly darker color than the calyx plates.

In this species the anal plates are very prominent, rising from the posterior basal in the form of a finger-like series, which makes a reverse curve toward the ventral side, the distal end going to the right. It is finely preserved in several of the specimens, but does not appear so plainly in Fig. 1, Plate IV, where it has fallen under the posterior edge of the large oral; but in Fig. 3 it is perfectly shown. It is composed of strong and solid plates, well rounded dorsally, and connecting at the inner side with the membranous integument of the disk, which is sometimes found folded longitudinally alongside of it. This anal appendage does not seem to be actually a tube, as I cannot detect any longitudinal opening or canal through it. In one specimen I find it standing apart from the other plates, and the inner side entirely enveloped in the membrane—thus indicating that the row of strong plates more probably served as a support for a soft tube or opening formed by the protuberance of the membrane itself.

The exact position of the anal opening has not been observed, but it was no doubt at or near the end of the anal series. So far as I can see, the distal end becomes merged in the perisome of the disk, and it is probable that the aperture for the hind gut was at that point. In all the specimens the structures are broken down and displaced in this part, being involved in the downfall of the large posterior oral, so that the exact fact cannot be ascertained. I have no doubt that the anal structure was substantially the same as in *Taxocrinus intermedius*, in which, however, the anal opening has not been definitely located.

In considering the significance of the disk of *Onychocrinus* as disclosed by these discoveries, we must refer to the observed course of development of the larva in one of the living representatives of the Flexibilia, *Antedon rosaceus*. Of this I take the following abstract from Dr. W. B. Carpenter's account[1] of this species in its Penta-

[1] *Philosophical Transactions*, 1866, p. 727.

crinoid stage, between the time of emergence from the embryo and that of casting off the stem, reference being had to the figures herein:

The animal consists in the first instance of the stem and calyx alone, not even rudiments of arms being distinguishable. The calyx completely incloses the visceral mass, its oral valves when drawn together meeting over the mouth, and when these open out it takes the form of an inverted bell. Its oral part is composed of five oral plates, the approximation of which forms a five-sided pyramid with its truncated apex pointing upwards—though they are usually erected as separate valves, to allow the oral apparatus to be projected from within them. The mouth of the bell, when the oral valves are expanded, is entirely occupied by the oral tentacular apparatus. The general aspect of the young Pentacrinoid, as seen with the tentacular apparatus retracted in a spirit specimen, is shown in Plate V, Fig. 1. The oral plates are triangular in form, their apices pointing upward, but capable of closing so as to form a five-sided pyramidal cover to the calyx (Plate V, Fig. 3). With the further development of the Pentacrinoid, a remarkable change takes place in the relative position of these orals. They do not increase with the other elements of the growing calyx. They continue to embrace the circle of oral tentacles, the diameter of which comes to bear a smaller and yet smaller proportion to that of the ventral surface of the disk; and thus it comes to pass that the circlet of oral plates detaches itself from the summits of the radials on which it was previously superimposed, and is *relatively* carried inward by the great enlargement of the circle formed by the latter—the space between the two series being now filled in only by the membranous perisome, which is traversed by the five radial canals (ambulacra) that pass out from the oral ring between the oral valves to the bifurcation of the arms (Plate V, Fig. 7).

Before the body of the Pentacrinoid drops off its stem, an incipient resorption of the oral plates is discernible, commencing along the margins of the apical portion, so that these plates lose their triangular form and become somewhat spear-shaped (Plate V, Fig. 7). This absorption continues in various degrees; sometimes the upper half of the oral plate disappears, and in other cases the marginal portions only of the upper part of the plate have been removed,

leaving a sort of central tongue projecting upward; finally, soon after the Crinoid becomes free, they completely disappear.

The condition presented by the disk of *Onychocrinus* may be considered to be somewhat approximate to that of the last stage of the *Antedon* Pentacrinoid before it casts off the stem, and before the orals are finally resorbed (Plate V, Fig. 7). In the irregularity in the size and shape of the orals in these fossils we may perhaps recognize some of the different stages of absorption in the *Antedon* larva as above described.

We may also compare the morphological condition of our disk with that of P. H. Carpenter's remarkable recent genus *Thaumatocrinus.*[1] His solitary specimen, of which I reproduce one of his figures (Plate IV, Fig. 6), was very small, probably in a young stage. If we imagine it in a more mature condition, with the orals pushed inward and made relatively smaller by the growth of perisome, and the anal tube more or less enveloped by it, we shall have a disk somewhat analogous to ours. Of course the enormous posterior oral of the *Onychocrinus* disk does not find a parallel in any of the recent tegmens. Its pronounced bilateral symmetry is a paleozoic characteristic, strongly marked among the Camerata and Inadunata, as well as in many of the Flexibilia. It is possible that the posterior oral is a madreporite, as has been found in many Cyathocrinidæ. It seems to be perforated with somewhat scattered pores in several specimens, one of which I figure, twice enlarged (Plate IV, Fig. 4). This may be something like the water-pores in the orals of *Holopus*, as shown in Carpenter's figure above cited (Plate V, Fig. 8).

Since obtaining the above-mentioned specimens, I have succeeded in exposing the disk of a specimen of *Onychocrinus exsculptus*, from Crawfordsville—a thoroughly distinct species. While by no means so perfect, it shows that the structure is substantially the same. I have also obtained another disk of *Taxocrinus*, from a much later horizon than *T. intermedius*, which exhibits the same characteristics as the latter species.

FURTHER REMARKS ON THE CRINOIDEA FLEXIBILIA

In a paper in the *American Geologist* for August, 1902 (pp. 88 ff.), I offered some suggestions looking to the systematic arrangement of

[1] *Philosophical Transactions*, Royal Society, Part III (1883), p. 919.

the Impinnata division of the Crinoidea Flexibilia, dividing them into two main family groups—Ichthyocrinidae and Taxocrinidae. Some of Angelin's Silurian genera, as stated at that time, were arranged with doubt. Since then I have received from Mr. G. Liljevall, of the National Museum at Stockholm—who has at my request made a careful examination of the Swedish material belonging to this group—a set of fine drawings of the principal specimens of Angelin's genera, embracing all the types figured in the *Iconographia Crinoideorum* that can be found, and some other specimens not heretofore figured. These drawings, made with the unrivaled skill and care which characterize all of Liljevall's work, have made clear some points hitherto obscure on account of the notorious inaccuracy of Angelin's figures, and have also led to some unexpected results. In view of the importance of some of these observations, and their bearing upon the classification of this group, I have thought it advisable to publish a brief account of them now as a preliminary note to the work upon it which I have in preparation.

It was shown in the paper above cited that in the family Taxocrinidae there is a progressive variation in the position of the radianal, similar to and somewhat parallel with that observed in the Inadunata, viz.: from a primitive position directly under the right posterior radial, to an oblique position under the lower left corner of that radial in the Silurian, and finally to complete elimination in the Carboniferous. It now appears that there is a similar variation and succession in the position of the radianal among the Ichthyocrinidae. *Anisocrinus* and *Clidochirus* prove to have a large radianal; in the latter in a radial position directly underneath the right posterior radial, as if it were the lower half of it, as in *Temnocrinus;* while *Lecanocrinus* and *Pycnosaccus* have it smaller, and located obliquely under the left part of the right posterior ray, as in *Gnorimocrinus*. *Homalocrinus* also has the radianal in the primitive position, but it is smaller than in the two first-named genera. In *Mespilocrinus* and other carboniferous forms it has disappeared altogether.

The greatest surprise, however, has been to find a somewhat similar condition among forms which have been referred to the genus *Ichthyocrinus*. The genus has been heretofore considered by everybody as the simplest of all, having a perfectly symmetrical calyx,

without anal or interbracial plates, and persisting in this simple form from the Silurian to the Carboniferous. It now develops that this is not true for the Silurian species. Liljevall, while making the drawings for me above referred to upon specimens in the Museum at Stockholm, called my attention to the fact that in all Gotland *Ichthyocrini* the right posterior ray has an extra plate, just like *Temnocrinus tuberculatus*. By cleaning the base of some specimens so that the infrabasals could be seen, he was able to locate the right posterior ray by its being in line with the small infrabasal. It was in this ray that the extra plate was invariably found, smaller than the radial, sometimes visible laterally and sometimes hidden by the column. Here, evidently, was also the radianal in its primitive position. I have much pleasure in according to Mr. Liljevall the credit for this sagacious observation of a fact which had escaped the notice of all of us.

This at once suggested the idea that probably the same thing would be found in the Silurian *Ichthyocrini* from England and America; and an examination of the published descriptions immediately furnished abundant indications of it as to the American species. Hall's figures and diagrams of *I. laevis*,[1] and of *I. simplex*[2] show an extra plate in one ray. So also do his figure of *I. subangularis*,[3] and Ringueberg's figure and description of his *I. conoideus*.[4] A similar condition was indicated in Weller's description of *I. subangularis*,[5] where he says the radials are "generally unequal," and "costals two, rarely three, in each ray." In all of these there appeared to be in one ray four primary plates, instead of three as in the others, though in none of them was the position of the infrabasals accurately shown, so as to determine which ray possessed the extra plate. Indeed, without special preparation the infrabasals cannot often be seen in this genus. Nevertheless, with the facts shown by the Swedish specimens, there seemed no reason to doubt that the irregular ray was here also the right posterior.

1 *Palæontology of New York*, Vol. II, Plate 43, Figs. 2a and 2e.

2 *Ibid.*, Plate 46, Fig. 2e.

3 *Twenty-eighth Report*, New York State Cabinet of Natural History, Plate XVI, Fig. 13.

4 *Annals*, New York Academy of Sciences, Vol. V, No. 6, p. 301.

5 *Bulletin IV*, Chicago Academy of Science, p. 146.

These observations suggested also the idea that, if this should prove to be the fact in the Silurian and not in the Carboniferous species, then we should have a further and most interesting example of evolution in the elimination of the radianal from Silurian to Carboniferous times, within what has been considered as a single genus. With a view to ascertaining the facts definitely, I undertook a careful examination of my specimens, with additional preparation, sometimes grinding off part of the base to expose the infrabasals; and I have also since then had in hand for study good specimens from the Niagara of Canada and New York, most obligingly loaned me by Mr. Byron E. Walker, of Toronto, and Dr. E. N. S. Ringueberg, of Lockport, N. Y. This examination gave the following results:

Silurian Species

I. pyriformis (?), from the Wenlock Limestone, Dudley, England: In a large and quite perfect specimen I removed the stem, and by grinding succeeded in exposing the infrabasals; along with which appeared a radianal under the right posterior radial. This is invisible in a side view, but appears on the flat part of the base, only half as large as the radials in the other four rays (Plate IV, Fig. 3). Another specimen of true *I. pyriformis* in my collection, and three others since examined in the British Museum, show the radianal.

I. laevis, from the Niagara: Eight specimens from New York and Canada show infrabasals and radianal (Plate VI, Fig. 1).

I. subangularis, from the Niagara: Five specimens from Indiana and Illinois show infrabasals and radianal (Plate VI, Fig. 2); and numerous others among the casts of *I. corbis* found at Milwaukee and Chicago which do not preserve the infrabasals, distinctly show the impressions of the radianal.

Carboniferous Species

I. burlingtonensis, Lower Burlington Limestone: Six specimens preserving the rays all around show uniformly a radial and two primibrachs, without any sign of a radianal (Plate VI, Fig. 15). Two of them have the infrabasals well preserved, one both externally and internally.

I. tiaraeformis, Keokuk Limestone, Tennessee: Besides the type,

I have five specimens suitable for this study—two from the original locality at White's Creek Springs, Tenn., and three from near Louisville, Ky. Four of them have all the rays visible, and they all show perfect symmetry below the first bifurcation, the rays having uniformly the radial and two primibrachs, without any radianal. In these specimens there is some irregularity in the secundibrachs, one having 4–4 in all rays, and the others having 4–4 in some rays and 4–3 in others. In another specimen the rays are not fully preserved, but the condition is such that, in addition to the radials and some primibrachs, they show the basals and infrabasals very plainly, both internally and externally, and there is no radianal. In the type specimen, however, from the Troost collection in the National Museum at Washington, which preserves all rays intact, there is an extra plate in one ray, which has radial and three primibrachs, while all the others have two primibrachs, with variations of 4–3 to 4–4 secundibrachs. The infrabasals are not visible, and it is impossible to judge whether the extra plate is in the right posterior ray or not. The lower plate in the ray having the extra one is of the same size and shape as the lower plate in the other rays, and does not exhibit the difference which characterizes it in the Silurian specimens. In view of the uniform absence of a radianal in all other Carboniferous specimens, I think we are warranted in considering the presence of an extra plate in this one as a case of sport—just as we have in some specimens an occasional straggling interbrachial.

In *I. greenei*, from the Keokuk Limestone of Indiana, only three rays are visible, each of which has the radial and three primibrachs.

What the condition of the genus was in the Devonian we do not know. It is supposed to occur in the Chemung of New York, but all the specimens that I have seen are too imperfect to afford any information. If any reader of this paper should possess a specimen of *Ichthyocrinus* from the Devonian, with the base or all five rays preserved, I should esteem it a great favor to be advised of the fact.

The result, therefore, of the examination of actual specimens considered to be *Ichthyocrinus* is:

1. All Silurian specimens, without exception, have a radianal in primitive position under the right posterior radial.

2. All Carboniferous specimens (with the solitary exception above

noted) have a perfect pentamerous symmetry below the first bifurcation, and thus have no radianal.

Hence we have in this form an evolution from the Silurian to the Carboniferous, just as is found from

Sagenocrinus to *Forbesiocrinus*,
Gnorimocrinus to *Taxocrinus*,
Clidochirus to *Mespilocrinus*.

The process here shown, substantially parallel with what takes place in the Inadunata, is the elimination of the radianal in paleontological time by rising, or being lifted upward, from beneath the radial, analogous to the migration and disappearance of the anal plate in the larval stages of *Antedon*, of which I shall have more to say later on. If these views are correct, it follows that the Carboniferous form should be separated generically from the Silurian. As *I. laevis*, from the Niagara, is the genotype of *Ichthyocrinus*, it seems proper to retain the genus for the Silurian species and any other that may prove to have a radianal. I therefore propose for the Carboniferous form, and all that may be without a radianal, the genus *Metichthyocrinus*.

As already intimated, *Anisocrinus* and *Clidochirus*, two of Angelin's Silurian genera, also prove to have an unsymmetrical calyx, owing to the presence of a radianal underneath the right posterior radial. In *Clidochirus* it is directly under the ray, in the position of an inferradial (Plate VI, Fig. 7). This is shown in Angelin's figure of *C. pyrum.*[1] The original to his Fig. 6, Plate XVII, which is a restoration from an imperfect calyx, and incorrectly drawn as to the part preserved, is a right anterior view of a weathered specimen of this species; the lower part of the calyx, showing the anal side, is figured herewith (Plate VI, Fig. 8). There is also a third specimen in the Stockholm collection which shows the characters perfectly (Plate VI, Fig. 7). The difference between the two genera is that *Anisocrinus* has the interbrachials all around, while *Clidochirus* has none except at the anal side. The radianal of *Anisocrinus* is not quite so regular in its position as in the other genera having this structure. In *A. interradiatus* it is large, and well underneath the radial. Angelin's figure of his only specimen, Plate XXII, Fig. 18, does not show any

[1] *Iconographia Crinoideorum*, Plate XXII, Fig. 23.

radianal, but it is perfectly developed in the specimen (Plate VI, Fig. 9), and also in another one since found. In *A. angelini* W. and Sp. (figured by Angelin as *Lecanocrinus macropetalus*) his first specimen[1] has no radianal, and the figure is correct in this respect; but the second specimen[2] has a very distinct radianal, situated obliquely under the left corner of the right posterior radial; while in a third specimen, found since Angelin, the radianal is large, and fully under the radial (Plate VI, Fig. 10). It is quite possible that the first specimen does not belong to this genus, as there is some difference also in the arms.

These two genera differ from *Homalocrinus* and *Calpiocrinus* in having very large basals. It is interesting to note that both of them occur in America. *Lecanocrinus greenei* of Miller and Gurley,[3] and *L. oswegoensis*,[4] both belong unquestionably to *Anisocrinus*. Miller and Gurley's figure of *L. greenei* shows nothing of the radianal, which is plain enough in the specimen, cut off from the lower left part of the right posterior radial (Plate VI, Fig. 11); but in the other species it is shown in their Fig. 16 (Plate VI, Fig. 12). The *Clidochirus* is an undescribed form from our western Silurian.

Liljevall's drawings also enable us to understand the rare genus *Calpiocrinus*, which turns out to be a very curious and extraordinary affair (Plate VII, Figs. 1–8). Angelin described it as having three basals and no parabasals, or, as we should say now, three infrabasals and no basals. Wachsmuth and Springer[5] were much puzzled by the fact that this genus, as described by Angelin, seemed to have but one ring of plates below the radials; but expressed the opinion that this ring of plates "is the analogue of the underbasals, and that the true basals, if not absent, are exceedingly rudimentary." Dr. Bather, on the other hand,[6] states that *Calpiocrinus* "has minute, often obsolete IBB, but fairly large BB." The facts now disclosed show that Angelin's description was wrong; but that Wachsmuth

1 *Ibid.*, Plate XIX, Fig. 3, and Plate XXII, Fig. 24.

2 *Ibid.*, Plate XIX, Fig. 4.

3 *Bulletin No. 8*, Illinois State Museum, Plate III, Fig. 28.

4 *Ibid.*, No. 4, Plate III, Figs. 15, 16.

5 *Revision of the Palæocrinidæ*, Part I, p. 38.

6 Lankester's *Treatise on Zoölogy*, Part III, p. 189.

and Springer's interpretation of the conspicuous ring of plates was substantially correct. As a matter of fact, there are two rings of plates below the radials—i. e., both infrabasals and basals; but the remarkable thing about it is that the infrabasals are developed to an extent and in a manner unknown in any other Crinoid. In many dicyclic forms the infrabasals lie within the ring of basals, abutting against them by their lateral faces; and they are naturally subordinate in size and position. But here they overlap the basals to such an extent as to sometimes wholly conceal them, and not only them, but also the radials, and even part of the first primibrachs (Plate VII, Fig. 6). In some cases two or more of the basals are visible as mere points (Plate VII, Figs. 3, 8); but usually only the posterior basal projects (Plate VII, Figs. 2, 4). In one specimen no basal at all is to be seen, and the large infrabasals appear externally to be directly surrounded by the radials (Plate VII, Fig. 5).

The three unequal infrabasals form a relatively enormous growth, far exceeding in size the basals, and enveloping them somewhat after the manner of the centrodorsal in *Thiollierícrinus* and other Comatulae. The actual relation of the two sets of plates is shown in specimens like Fig. 6, Plate VII, where the infrabasals have been partly removed, and the basals become plainly visible beneath them, five in number. Thus the basal elements of the calyx are the same as in the group generally—3 IBB, and 5 BB—and the small infrabasal is usually located, as it should be, under the right posterior ray. In addition to the information furnished by Liljevall from the specimens at Stockholm, I have several good specimens of this genus in my own collection, which fully confirm the foregoing observations. There remains no longer any doubt of its real structure, and the genus must therefore be considered as representing a definite, though extravagant and therefore short-lived, modification of the Crinoid plan, in a direction not heretofore noted.

This condition seems to be an exaggeration of that which obtains in many of the Flexibilia, where the infrabasals have a tendency to overlap the basals like a column plate, as in *Forbesiocrinus* and *Taxocrinus*. In these cases the union with the column seems to be stronger than with the calyx; the infrabasals are frequently fused with the top columnal, and remain firmly soldered to it when the column is

detached from the calyx.[1] That is what has happened in the specimen figured herein (Plate VII, Fig. 20), where the infrabasals have separated from the calyx in this manner. This feature is the result of the general fact, discovered by Wachsmuth and Springer,[2] and accepted by subsequent authors, that in the Flexibilia generally the top columnal is not the latest formed, as in the Camerata and most Inadunata, but remains as a persistent proximale. This has been believed to be a fundamental character, evidencing the independent nature of the group—though the proof of its universality is, in my opinion, not complete, and there are apparent exceptions to it. The remarkable example of regeneration mentioned by me in my former paper on this subject,[3] where the calyx of a *Taxocrinus* was restored by new growth upon the infrabasals and one basal, is strongly confirmatory of this idea, and suggests that in this group the axial organ as the seat of vitality in the animal, was located very low in the calyx—i. e., within the infrabasals and extending down into the proximal part of the column.

Homalocrinus, which Angelin founded on a single species, *H. parabasalis*,[4] is of a similar type, but the basals are larger and not so much concealed by the overlapping infrabasals (Plates VII, Figs. 9, 10, 11). I was at first disposed to consider it as congeneric with *Calpiocrinus*, until Liljevall's careful study of the type specimen brought to light a small radianal lying beneath the right posterior radial. Then it occurred to me that this was the condition of certain specimens from the Wenlock Limestone of Dudley, England, which had for a long time puzzled me—and for which in my former paper I had suggested the name *Leiocrinus*—and that they would fall nicely under *Homalocrinus*. They accentuate the differences between *H. parabasalis* and *Calpiocrinus*, having larger radianal and more prominent basals. I give figures of two of the specimens (Plate VII, and Figs. 12, 13), and propose for them the name *Homalocrinus dudleyensis*. So far as I know, these two genera are the only Crinoids in which such a peculiar development of the infrabasals is found.

There is a notable difference between them in the arm structure—

[1] *North American Crinoidea Camerata*, Plate II, Fig. 4*b*.

[2] *Ibid.*, p. 39. [3] *American Geologist*, Vol. XXX, p. 97.

[4] *Iconographia Crinorde'rum*, Plate XVI, Fig. 29.

Calpiocrinus having twenty main arm branches or trunks, about equal, each pair bearing ramules inside the dichotom; while *Homalocrinus* has ten such main branches. The first, or lowest, ramule is usually the largest, and may sometimes branch again. Variations in this respect give rise to intermediate forms, and while well-marked specimens of the two genera are strikingly distinct, it is easy to see how the two arm characters shade into one another. In *C. fimbriatus* (Plate VII, Fig. 1) it will be seen that the ray bifurcates into two equal divisions, and each of these divides again into two main branches or trunks of about equal size, from the inner side of each of which are given off three or more lateral ramules. In *H. parabasalis* (Plate VII, Fig. 9) and *H. dudleyensis* (Fig. 12) the first bifurcation in the ray produces two main arm branches having similar ramules, of which the lower one is the largest. If this lower ramule increases further, until it approaches the size of the outer branch, and also begins to give off in turn subordinate ramules, then we shall have the condition, approximately, of Fig. 1. Thus we may expect to find intermediate stages of this progression; and when the lower ramule of the ten-branched form becomes considerably enlarged, we are in doubt whether upon this character to call it *Homalocrinus plus*, or *Calpiocrinus minus*. And then comes the old question: Shall we throw them all into one genus because of the connecting links, or maintain the genera upon their typical forms? Of course, the correlation of the radianal, if present, will avoid this difficulty; but I find this to be quite unequally developed in the English forms of *Homalocrinus*, and it is probably so in the Swedish—being so small in the type specimen of *H. parabasalis*. In the former some of my specimens have it only half the size of the radial, some about equal to it; and in some, not otherwise distinguishable, I cannot see it at all. I think the difference in this respect may be partly due to the unequal development of the infrabasals, which may sometimes conceal the radianal, which in this form is located wholly within the ring of basals, as in *Sagenocrinus*. This may also be considered as an interesting case showing how, under the influence of an extravagant modification, characters otherwise important were greatly overshadowed, and a close and rapid transition occurred, tending to produce an intermingling of such characters.

Phillips' genus *Euryocrinus*, which has been heretofore considered

a synonym of *Ichthyocrinus*, may now be assigned a definite place in the analysis of the genera. Thanks to the courtesy of Dr. Bather, I have recently had the opportunity to examine the type specimens, now in the British Museum; and they demonstrate very clearly the generic distinctness of this form. It has the regular dicyclic base of the Flexibilia, with 5 BB and 3 IBB—the latter more or less atrophied, or resorbed by the very large axial canal; and it has a series of large anal plates, completely filling the posterior area, together with a small development of interbrachial plates. It has the habitus of the *Ichthyocrini*, and stands close to *Parichthyocrinus*, from which, however, it is well distinguished by the anal structure.

I am also now enabled, by the aid of Liljevall's drawings and some interesting specimens in the British Museum, to treat more definitely the genus *Pycnosaccus*, which was formerly placed as a probable synonym under *Lecanocrinus*. It has fairly large interbrachial areas, which are apparently without well-defined plates, such as are in *Anisocrinus*, but were evidently filled by small, irregular plates which are not preserved in any of the specimens thus far seen. The calyx as observed is strong, and much wrinkled or folded exteriorly. It also frequently has but a single primibrach.

Cleiocrinus, from the Lower Silurian of Canada, which was before arranged with this division of the Flexibilia, may now be left out of it, except as a probable transition form. From an investigation I have recently made of all the known material, this proves to be an even more extraordinary and anomalous genus than *Calpiocrinus*, being probably an intermediate form between the Camerata and the Flexibilia. It has the pinnulate arms and five infrabasals of the dicyclic Camerata, combined with the pliant calyx, with plates united by loose suture, of the Flexibilia.[1]

I exclude from the list of Flexibilia the genus *Rhopalocrinus*, which may be considered as an intermediate form between the Flexibilia and the Inadunata. It has a strong ventral tube, rising high up between the arms. It lacks the pliant calyx of the former group, but rather resembles a dicyclic Symbathocrinoid, and would readily fall under the Inadunata but for the presence of a slightly developed interbrachial system.

[1] *Memoirs*, Museum of Comparative Zoölogy, Harvard, Vol. XXV, Part 2.

Professors Waagen and Jahn, in Vol. VII of the *Silurian System of Bohemia*, have described a new genus, *Caleidocrinus*, from Stage d 4 of the Bohemian section, which they place near the Taxocrinidae of Angelin, and which Mr. Bather[1] assigns to the Flexibilia Impinnata, and considers to be "a genus that approaches the common ancestor of *Ichthyocrinus* and *Taxocrinus*." Through the kindness of Professor Jahn, who made a special trip to the locality near Zahoran for me, I have been favored with some specimens of *C. multiramus* in as good condition as they are usually to be obtained. They occur in a schist, and all specimens thus far found are so flattened by pressure that none of them show all five rays, and I doubt if it is certain whether the anal side is distinct or not. The condition of preservation is such as to render observation on some points very uncertain. Messrs. Waagen and Jahn[2] say of this:

> The skeleton and elements constituting the body of these sea lilies are changed into a ferric hydrate. By reason of this change there exist only the negative impressions of half the calyx, which are filled with a powder of ferric hydrate.

They state that the figures on Plate 63 are very defective, and they give other figures in the text, partly of the same specimens and partly from better specimens. Even of these text-figures, however, they say on p. 109:

> The preservation of the interradius (*ir*, Figs. 276—316 of the text), and of the anal interradius (*a*, Figs. 276–316 in the text), is so defective that if we can, in some cases, observe the position of the plates which compose them, it is never possible to determine their number.

I have six good specimens in the condition described by the authors, viz., impressions in the matrix filled with powder of iron oxide; and one rather larger than usual in which, by rare fortune, the skeleton of the Crinoid is preserved intact. I have also wax casts of the specimens from which Figs. 1–2 and 11–14 of Waagen and Jahn's work were made, kindly sent to me by Professor Dr. Perner, of the Royal Museum at Prague. In none of these have I been able to identify satisfactorily any interbrachial (interradial) or anal plates. Not having seen all the specimens on which the figures are based, I do not deny the existence of such plates; but I wish to suggest

[1] *Annals and Magazine of Natural History*, July, 1900, p. 112.

[2] *Op. cit.*, p 107.

that in specimens preserved as these are it is extremely difficult to determine such structures with certainty. Many foreign bodies may become lodged between the rays which might, in the chemically changed condition of the fossils, be mistaken for small, irregular plates. One may even mistake for interbrachials what may be only fragments of arms, as has actually cccurred in one case I know. In my specimen with the substance of the Crinoid preserved the radial and brachial plates are well defined, and there is certainly no sign of any plates meeting their margins between the rays. Assuming them to exist, however, as figured by the learned authors, they may be taken to form part of a flexible integument, and the structure would be in a condition analogous to that of the Carboniferous genus *Niptero-crinus*, although otherwise there is no resemblance between them.

Nothing is known of the base; whether it is dicyclic or monocyclic cannot be ascertained from the specimens. The habitus of this form seems to me rather like that of the Inadunata, from which it is separated only by the supposed interbrachial structures. It is certainly a strange and interesting genus, as to which we may well wish for more information. If it had been found in the Jurassic, instead of the Ordovician, I think no one would have hesitated to place it among the Pentacrinidæ.

Dr. Bather bases his conclusion as to the ancestral character of this form upon the statement that it is "older than any flexible genus hitherto known, and the interest is enhanced when we see how its structure accords with its age in the eyes of the evolutionist;" and that "Flexibilia have not hitherto been known earlier than the Wenlock age." In making this statement he must have overlooked the specimens of *Taxocrinus* described by Billings under *Lecanocrinus elegans* and *L. laevis*,[1] which are much older than the Wenlock, and at least as old as the stage of *Caleidocrinus*. They occur in the Trenton Limestone of the Lower Silurian, or Ordovician, at a horizon which has been considered by geologists as substantially equivalent to the Bala of England, which Bather takes to be about equal to the Stage d 4 of Bohemia. And it is, of course, much older than the Wenlock, which is the age of the Upper Silurian, approximately equivalent to the Niagara of America.

[1] *Canadian Organic Remains*, December, IV, Plate IV, Figs. 3, 4.

In the second family group, as formerly defined, subsequent observations have led me to make some important modifications of the arrangement heretofore proposed by me. It has long seemed desirable to find some basis for separating the Silurian species of *Taxocrinus* from the Carboniferous. Considering the changes that have taken place in other types of this group, and especially since the discovery of the facts above stated as to the *Ichthyocrini*, it seemed to me to the last degree improbable that such a form as *Taxocrinus* should persist from the Lower Silurian to the latest Subcarboniferous, without any modification of more than specific importance. Yet upon the basis of any of the characters hitherto regarded as important in this group I was unable to find satisfactory ground for distinction. I was at first strongly disposed to believe that the Gotland species must all, if correctly observed, prove to have an unsymmetrical calyx—that is, with a radianal—and thus belong to *Gnorimocrinus*. But a careful re-examination by Mr. Liljevall of all the specimens at Stockholm, with detailed drawings of each, has convinced me that Angelin's *T. rigens* and *T. oblongatus* have no trace of a radianal. The type specimens of *T. elegans* and *T. laevis*, from the Lower Silurian of Canada, do not show the anal side, but when discovered I should expect to find a radianal.[1]

Finally, however, the solution presented itself in a very simple matter, which has been overlooked hitherto in all researches upon the classification of this group, but which, upon consideration, appears to be of considerable importance. It lies in the condition of the rays below the first bifurcation—that is, of the brachials of the first order. On account of some irregularity in a few cases noted by early observers, it has been handed down as a tradition, and religiously observed, almost since the time of Phillips, that such irregularity in the branching of the rays was a characteristic of the whole group. This fact seems to have diverted attention from the real significance of this structure. In the *Revision of the Palæocrinoidea* this opinion was expressed, and in proof of it allusion was made to the differences in the rays of *Ichthyocrinus*, which are discussed herein, and shown to

[1] Since the above was written, specimens of both species have been found showing the posterior side, and each has a large radianal in primitive position under the right posterior ray.

be due to the presence of a radianal uniformly in one ray; and to the case of *Forbesiocrinus agassizi*, which will be considered later. I have often heard Wachsmuth emphasize the statement that not only are there irregularities in the rays, but that such irregularity was a positive character of the group.

If we take a specimen like *Taxocrinus affinis* Mueller,[1] we see that the ray bifurcates on the second plate above the radial; or, in other words, the ray has two brachials of the first order, or primibrachs. Examining then the figure of *Taxocrinus splendens* M. and G.,[2] from Crawfordsville, Ind.—the best known Carboniferous species, and found under other names in collections the world over—we shall find that the bifurcation of the ray occurs on the third plate above the radial; that is, it has three brachials of the first order, or primibrachs. The first of these plans is that which prevails throughout the Camerata, with a few exceptions, some of which can usually be explained by the anchylosis or syzygial union of two plates. It now proves to be a fact that it is also the structure of almost every one of the Silurian and most of the Devonian forms of the Flexibilia, with a very few exceptional cases, some of which I believe may be traceable to abnormal specimens. It follows feebly down into the Carboniferous in the genera *Synerocrinus*, *Wachsmuthicrinus*, *Mespilocrinus*, and *Metichthyocrinus*, all of which are rare fossils. It ceased in the Paleozoic, so far as we know, with the Keokuk Limestone, nothing of that form having been seen from the Warsaw, St. Louis, or Kaskaskia, beyond a few individually exceptional cases. Afterwards it appears to have resumed its sway in the group, for it prevails through the Mesozoic and to the present time in the great genera of the Flexibilia Pinnata—*Apiocrinus*, *Millericrinus*, *Uintacrinus*, *Antedon*, and *Actinometra;* the two primibrachs in the later two genera being sometimes united by syzygy.

The second plan, while it may be exceptionally indicated by a few cases in the Silurian and Devonian, became the leading feature of the Carboniferous Flexibilia, where it is conspicuous in numerous species of the widely distributed genera *Taxocrinus* and *Forbesiocrinus*, from the Waverly to the Kaskaskia; *Parichthyocrinus* in the

[1] *Mon. Echinod. Eifler-Kalkes*, Schultze, Plate 4, Fig. 2.

[2] *Bulletin No.* 8, State Museum of Illinois, Plate 5, Fig. 3.

Burlington and Keokuk; until the culmination of the group in *Onychocrinus*, some species of which regularly add another primibrach. It prevailed exclusively during the Warsaw, St. Louis, and Kaskaskia, after structure No. 1 had disappeared.

Occasional abnormal specimens occur in these genera, but they are rare, and no more than might be expected to occur in a structure so powerfully modified as this. In order to test the possible importance of these exceptions, I tabulated the facts as observed in two abundant species, representing the two leading genera of plan No. 2, with three primibrachs, viz., *Forbesiocrinus multibrachiatus* L. & C. (not the Crawfordsville species erroneously so labeled in many collections, but from a different horizon and locality), and *Taxocrinus spendens* M. & G. (which is the well-known Crawfordsville species labeled in some collections *T. multibrachiatus*, and in some *T. Meeki*). Both were prolific species, flourishing abundantly in two different horizons and localities—thus furnishing the right conditions to show irregularity if it exists. Of these I have a large number of specimens in which five rays are exposed. In thirty such specimens of *F. multibrachiatus*, ranging from very young to adult, all have the regular three primibrachs throughout, except three specimens, which have two primibrachs in one ray. In *T. splendens*, out of eighty-nine specimens—

77 have the regular	3 IBr throughout,
4 have	4 IBr in one ray,
6 have	2 IBr in one ray,
2 have	2 IBr in two rays.

All other rays of these are regular.

Variations as great as this are to be found in the strongest characters of almost any group in nature. Out of a large number of *Pentremites godoni* I have no less than thirty-two specimens with only four rays, and seven with six rays. I have a *Taxocrinus*, otherwise perfect, which has only four rays—there being no sign whatever of a fifth. The seeker after good luck will find by diligent search more four-leaved clovers than he will exceptions to the regular brachial arrangement of *Taxocrinus* and *Forbesiocrinus*.

The case of *Forbesiocrinus agassizi* has been cited as a decisive example of irregularity in this group, being said to vary from one to

three primibrachs. I have never seen a specimen with only one, although it might happen as a mere abnormality; but the case is a most interesting one upon the actual facts. This species, from the Burlington Limestone, systematically and regularly departs from the brachial arrangement of all other described *Forbesiocrini*, in having but two primibrachs. It is a rare species, and specimens are especially rare in which all rays are exposed; but usually at least three are visible, enabling us to see the prevailing type. I have thirteen specimens, and have observed seven in other collections, all of which show two primibrachs in the visible rays. There is another form occurring still more rarely in the Burlington Limestone which has the normal arrangement of three primibrachs. It is considerably smaller than *F. agassizi*, but strongly resembles it, and has hitherto been assumed to belong to it. It might be treated as of the same species, which would thus exceptionally embrace representatives of structures elsewhere widely distinct; or, what is perhaps the more rational view, good reason may be given for separating *F. agassizi*, both specifically and generically.

In *Taxocrinus* also there is some irregularity of this kind among certain Devonian species; that is, some individuals have two primibrachs, while others of apparently the same species have three. In a specimen of *Taxocrinus intermedius* from the Kinderhook two rays are irregular, and in the type of *T. nobilis* from the Mountain Limestone, one. Here the Devonian and Lower Carboniferous may be considered the transition period, in which the three primibrachs were being established in the genus. There is also to be seen in occasional specimens in the Kaskaskia a tendency toward reversion to the two-primibrach structure.

Ichthyocrinus greenei, of the Keokuk Limestone, is the only example of *Ichthyocrinus* or its carboniferous representative with three IBr in more than one ray. It is known only from a single specimen, which does not expose the anal side; and we cannot be certain of its generic relations, notwithstanding its close superficial resemblance to the typical *Ichthyocrini*.

I am not concerning myself, however, with the few exceptional cases which may be found; but if anyone will examine such a series of the four leading genera above mentioned as I have before me, with hun-

dreds of specimens of wide geographical distribution and great vertical range, he will see that there is not the slightest doubt of the validity of the distinction between the two plans of structure. If irregularity in the rays were a prevalent character, we would expect, in species of many genera, numerous variations in the number of primibrachs in different rays of the same individual. But we do not find the number varying indiscriminately among the rays; as a matter of fact, such cases are extremely rare. Besides those above noted, I have seen such variation in scarcely a dozen specimens among all the genera, and these are mostly confined to a single ray. We do not find, to any appreciable extent, intermediate forms—not, indeed, so many as might be expected. *Lecanocrinus*, and its allied form *Pycnosaccus*, exhibit some irregularity in a tendency to a single primibrach instead of two. The few known specimens of *Pycnosaccus* vary from one to two plates, both in the primibrachs and secundibrachs. The Silurian species of *Lecanocrinus*, in which the rays are preserved in many specimens, show very few exceptions to the rule of two IBr; but in the Devonian, on the eve of the extinction of the genus, there appears to have been more variability, although our materials for testing it are very meager. Of Schultze's *L. roemeri*, in the only two specimens I know preserving the arms, the number of IBr varies as follows: No. 1, 2–1–1–1–1; No. 2, 2–1–2–2–1. There is also a specimen from the Silurian of Sweden, something like *Calpiocrinus*, which has one IBr all around except in the posterior ray, where an additional one appears, perhaps a radianal. These cases may be explained by supposing the two IBr to have been coalesced by syzygial union, as occurs among the living Comatulae. In *Onychocrinus ulrichi* there is some variation from the rule of four IBr, some rays having three, and others five. This was at about the extinction of the group, of which *Onychocrinus* represents the most extravagant development.

Of course in the Silurian those species with a primitive radianal have a partial equivalent of three IBr in the right posterior ray; but that is constant, and is otherwise accounted for; and it does not affect the rule which prevails throughout the four regular rays. What was the morphological process by which this modification took place, I am unable to explain. The developmental history of

the group indicates a tendency to get rid of the extra plate in the right posterior ray, if we have been right in considering that plate—both in this group and in the Inadunata—as a radianal. But the change was not characterized by any indiscriminate individual variations; it must have taken place directly from one structure to the other, through mutations in species and genera. Out of twenty-six specimens of *Temnocrinus tuberculatus* showing the posterior ray, but a single one fails to show the radianal as I have described it.

In the Silurian, the plan of two IBr prevailed almost exclusively—only two generic forms, represented by *Gnorimocrinus loveni* in Sweden, and *Taxocrinus orbignii* in England, having three IBr throughout. One abnormal specimen of *Gnorimocrinus expansus* has three IBr in one ray, and one of *G. tubuliferus* has it in at least three rays. So far as I know, these are all the exceptions in the Silurian. The change was more notable in the Devonian, where some species have both two and three IBr and about one-third of the species heretofore referred to *Taxocrinus* appear with three IBr throughout. The *Taxocrinus* with two IBr persisted into the base of the Carboniferous with one or two species in the Kinderhook and Waverly; but from there on the three IBr structure became universal in this and related genera. The few exceptional cases we know in individual specimens do not fill the gap between the two structures. It was a decided morphological change, affecting the entire brachial system, and as to the *Taxocrini* it took place chiefly in the Devonian.

It follows from these considerations that the Silurian and most of the Devonian species of *Taxocrinus* should be separated generically from those of the Carboniferous. Since *T. tuberculatus* has been removed to form the type of *Temnocrinus*, on account of the possession of a radianal, there remain three species originally referred to the genus by Phillips: *T. nobilis*, *T. macrodactylus*, and *T. egertoni*. In discussing them under his first name, *Isocrinus*,[1] he says that *T. nobilis* and *T. macrodactylus* have four "costals." It is clear that he includes what we now call radials and primibrachs, for on p. 29 he says: "the pentagonal columnar joint is surmounted by five plates (the pelvis of Miller), alternating with which, and above them, are

[1] *Pal. Foss. Cornwall*, p. 30.

five rows of broad costal and scapular plates, four in each, the last being cuneiform." As *T. nobilis* and *T. macrodactylus* have hitherto been taken as the typical forms of the genus, and according to Phillips' diagnosis they possess the brachial structure No. 2, it seems proper to retain the name for the Carboniferous species and such Devonian or Silurian ones as prove to have this structure. For those species of *Taxocrinus* having the original structure of two primibrachs I propose the genus *Eutaxocrinus*, including provisionally the Silurian *T. oblongatus* and *T. rigens*, which are probably one species, and tend toward *Dactylocrinus* in the arm structure.

In attempting to arrange the genera of the Flexibilia into families, or other subgroups, we have to choose between several kinds of modification on which to base them. We know the life-history of one genus of the Flexibilia Pinnata, viz., *Antedon*. Considering that to represent, in a general way and to some extent, the phylogenetic history of the group, we may assume that its ancestral form would be something like the early larval stage of *Antedon*, with the addition of a radianal, of which no trace or suggestion has yet been found in the embryological researches on that genus, as I understand them. This would give us a dicyclic Crinoid, with a radianal; an anal plate between the posterior radials; two primibrachs, the second one axillary and followed by arm branches; and the ventral side surmounted by a closed pyramid of oral plates. I have attempted to represent the dorsal side of such a hypothetical Crinoid by Fig. 9 on Plate II. The lines of modification from such a form on the dorsal side would be:

a) In the radianal, by migration upward.

b) In the anal system by (1) extension upward in vertical series not connected with brachials, and replacement laterally by perisome; (2) increase upward and laterally in connection with the brachials; (3) elimination of the anal plate.

c) In the brachial system by (1) increase in the number of primibrachs; (2) variation in the mode of branching of the higher brachials or arms.

d) In the interbrachial system, by growth and multiplication of supplementary plates between the rays.

On the ventral side we might expect modification in the same way that we see in *Antedon*, viz., a growth of perisome between the radials and orals, gradually separating the latter plates from the raidals and carrying them inward toward the center. This would give the condition found in *Onychocrinus* and *Taxocrinus;* but the cases in which these structures are preserved in the fossils are too few to enable us to trace any of the successive changes.

a) The first of the above modifications of the dorsal side has been already discussed, both in this and my former paper; and it has been shown that there are to some extent parallel modifications of this character in the two families as formerly defined, which might form the basis of some lesser groups. But the radianal was early eliminated in this group, being known only beyond the Silurian in two Devonian species, and modifications on this line do not cut much figure in the delimitation of the families. There are still some troublesome questions of interpretation among the Swedish species, owing to irregularities. Several of them are represented by only a single specimen, and this in some cases abnormal. These cases will be left for consideration hereafter in greater detail, in the hope also that the discovery of further specimens will throw new light upon them.

b) The generic distinctions based upon the other modifications of the posterior, or anal, area, coming under the second category, are really very striking—more so than can be well expressed in terms of brief analysis. Aside from the matter of the radianal, there are two plans of structure of the anal area, which run side by side from the Silurian to the Carboniferous. They start with the primitive anal plate of our supposed ancestral form, and diverge upon the two lines 1 and 2 indicated above.

1. The first of these plans is one which represents a solid support or backing of an anal tube. It is marked by a vertical row of strong, rounded plates, originating on the posterior basal, rising with a very gradual taper to a considerable height between the rays, and having the appearance of a small, rounded arm. It is connected with, or rather seems grown into, the pliant integument of small, irregular plates which formed the perisome, or ventral covering in this group.

As I have shown by the tegmen of *Onychocrinus*, the perisome developed between the radials and the orals, carrying the latter relatively inward until, instead of covering the whole ventral side as in the very early *Antedon* (Plate V, Fig. 3), they occupied only a small space in the center of the disk, into which the ambulacra converged after traversing the perisome (Plate IV, Fig. 1). In the present modification of the anal side it would seem as if the perisome began to grow with similar energy toward the dorsal side and down between the rays, so that it encroached upon the anal plate on either side as far as the posterior basal; while the upward extension of that plate took the form of a simple vertical series of rounded plates. Hence this armlike row of anal plates is usually found, in well-preserved specimens, bordered upon one or both sides by small, irregular plates, which were a part of the perisomic integument lying between them and the adjacent rays (Plate IV, Fig. 5). This plated integument, in addition to being pliant, was also very fragile, and its preservation in the fossil state is very uncertain and irregular. Sometimes it evidently fell to pieces when exposed between the rays, and no trace of it is found preserved; sometimes it was folded deeply inward between the rays, and so covered with matrix that it has not been observed in the fossils. This has often led to misconception of the real structure, and to misrepresentation of the facts in illustrations. For instance, it was at one time a matter of dispute whether the genus *Taxocrinus*, as then supposed to be represented by *T. tuberculatus* from Dudley, possessed any interbrachial connection between the rays, beyond a possible single plate. Proper cleaning now discloses, in many specimens of that species, the integument of small plates rising high up between the rays and their divisions. The characteristic appearance of this armlike series of anal plates, and also of the perisomic integument, is well shown in Wachsmuth and Springer's figures of *Taxocrinus intermedius*,[1] and also in the various figures of *Onychocrinus* herein (Plate IV).

Sometimes the rays lie so close together that they touch the anal series on both sides, and the bordering integument is thus folded inward so that it cannot be seen from the exterior. Nevertheless,

[1] *Proceedings*, Academy of Natural Science, Philadelphia, November, 1888, Plate XVIII.

the anal plates usually preserve their rounded appearance, and do not seem to form part of the calyx wall, or to be suturally connected with contiguous rays. Such cases as this give rise to difficulties of interpretation, because these are some forms in which the anal plates rise into a single vertical series connected by suture with the adjacent brachials, and flush with them. These must be distinguished from the cases just alluded to, where there is a rounded, armlike row of plates, so closely crowded by the rays that there is neither any part of the integument visible, nor any vacant space on either side, but which were evidently not joined to the brachials by suture. Both cases would answer the description "anals in a vertical series," and yet they undoubtedly represent the two distinct plans, which here, as elsewhere, run into perplexing transition forms.

The armlike row of plates, while not tubular, but on the contrary formed of thick and solid plates, is supposed to compose the dorsal support of an anal tube, formed by the outward growth of the perisome caused by the extrusion of the rectum. If we sometimes in descriptions call this row of plates "tube-plates," or the "anal tube," it must be understood as a conventional term—used by many former writers in this sense—to avoid circumlocution, and not as implying that the plates themselves are hollow, or strictly form the wall of a tube.

Now the position of this row of plates shows in a striking manner the effect of that strange influence which has modified the bilateral symmetry of almost every genus in this entire group. The small infrabasal is almost invariably located under the right posterior ray; the radianal originates under the right posterior ray; it migrates from this position upward until it disappears, but always to the right of the median line; if the arms have an asymmetrical distortion, it is to the right, never to the left. And so this vertical series of anal plates is affected by that tendency, which persists long after the radianal has disappeared. The posterior basal on which it rests is excavated into a sort of shallow socket, like the articulating facet of a radial, on the right shoulder of the plate, so that we will usually see a small tongue or angle of that plate rising up to the left of the base of the anal plate higher than to the right; or, if the socket-like excavation is not so plain as this, the upper edge of the basal is distinctly sloped to the right.

Not only so, but the anal series itself leans to the right, so that the vacant space, or the plated integument if it is preserved, is always widest at the left; and the anal plates are sometimes found firmly cemented by pressure to the side of the right posterior ray, leaving no other plates visible at that side, and giving an appearance of sutural union which must be guarded against in studying these fossils. The shape and position of this anal row of plates are subject to much variation, owing to pressure in fossilization, but the dextrorse asymmetry is almost the invariable rule. There does not seem to be in this form any special equivalent of the anal *x*. It would naturally be the lowest plate, resting on the posterior basal—the original plate of the *Antedon* larva, or of our supposed prototype—but it has been so encroached upon by the growth of perisome at the sides that it is relatively small, and the plates of the series show only a gradual taper from the proximal end upwards.

This plan of anal structure began in the Lower Silurian, and is found in the Taxocrinoid genera, with or without a radianal, from *Eutaxocrinus* and *Gnorimocrinus* in the Silurian, to *Taxocrinus* and *Onychocrinus* in the Carboniferous, surviving until the Kaskaskia, long after the other plan was extinguished. Being thus so characteristic of that line of genera, it may well be called the Taxocrinus plan. It has persisted to the present time, being found in a very characteristic form in *Thaumatocrinus* (Plate IV, Fig. 6).

2. The second plan is that of a simple extension of the anal system by the addition of other plates of similar solid nature to that of the original plate, and which are joined by sutural union to the adjacent plates of the posterior rays, and also with each other; so that, as far as they extend upward, they are incorporated into the calyx walls in the same manner as the plates of the other interbrachial areas. The posterior basal is either simply truncate, followed by one plate; angular, followed by two plates; or truncate with sloping shoulders, followed by three plates; but in each of these cases all the plates, and others of a similar nature succeeding them, form by sutural union (of course of the loose order characteristic of the whole group) part of the calyx wall.

This form of anal structure is found from the Silurian to the Carboniferous. The primitive stage of it is found in such genera as

Lecanocrinus (Plate VI, Fig. 13), and *Anisocrinus* (Plate VI, Fig. 10), in which the posterior rays arch over the anal plate, leaving no vacant space above it. In *Calpiocrinus* we see its simplest extension by the addition of single plates in succession above it (Plate VII, Fig. 7). In *Temnocrinus* we have a further modification by the addition of two or three plates abutting on the anal (Plate VII, Fig. 15). The development was rapid, for in another Silurian genus, *Sagenocrinus*, in which the dextrorse asymmetry caused by the presence of a radianal is still a feature, we have a perfect example of this plan in its fullest extension, where the anal area, following upon an angular posterior basal, is completely filled to the height of several orders of brachials, with solid plates, forming a regular continuation of the calyx wall. Because of its remarkable development in that genus, this form of anal structure may appropriately be called the Sagenocrinus plan. It is carried forward with equal perfection into the Carboniferous by the genus *Forbesiocrinus*. in which the radianal has been eliminated; and it ends in the Keokuk and Warsaw with species in which the asymmetry of *Taxocrinus* forms without a radianal has nearly disappeared, and the bilateral symmetry of the calyx is almost perfect. In most cases, however, asymmetry may be seen in the longer slope of the right shoulder of the posterior basal (Plate VII, Fig. 20). Where the posterior basal is truncate, the succeeding plate may be taken as the anal x, but where it is angular, as is most frequently the case, the anal x is apparently split in two, giving rise to two or more series of other plates above. While there are thus a few cases, as indeed we find also in the Silurian in forms like *Calpiocrinus*, which seem to be bilaterally symmetric, yet it is a fact that the dextrorse aysmmetry remains also as a general characteristic of this form as well as the Taxocrinus form. If the posterior basal is angular above, the right sloping face is generally the longest, and the series of plates following it a little the largest; if it is truncate and followed by one large plate which is angular above, the same remark may apply to the second plate; if it is truncate with sloping shoulders, the series from the right shoulder usually seems a little the stronger, and rises higher along the ray than the others.

Between such genera as *Calpiocrinus*, *Temnocrinus*, and *Sagenocrinus* there are considerable variations of this plan; but throughout

its entire range—except in certain peculiar transition cases to which I will allude later—there is no suggestion, in the external form, of any such structure as an anal tube.

Under this form, as well as the first, the modification reached the phase of the entire disappearance of the anal plates, first in the Silurian without disturbing the radianal, as in *Ichthyocrinus*, and afterwards in the Carboniferous with complete elimination of that plate, as in *Metichthyocrinus*.

Looking at these well-marked examples of the two plans, one cannot fail to be impressed with their complete distinctness as they stand side by side in the Silurian (Plate VII, Figs. 16 and 18), and in the Carboniferous (Plate VII, Figs. 17 and 20). They run a somewhat parallel course during the greater part of the paleontological history of the group, but not to the end. The Sagenocrinus plan ceases with the genus *Forbesiocrinus* in the upper part of the Keokuk or Warsaw Limestone, while the Taxocrinus plan survives to the last in the genera *Taxocrinus* and *Onychocrinus*. The latter is thus the one character connected with the anal structures which survived from the Lower Silurian to the extinction of the group in the higher Carboniferous, and is continued to the present time in one genus of the Flexibilia Pinnata. Only one specimen belonging to the Flexibilia Impinnata is known from rocks later than the Kaskaskia, and that is an Ichthyocrinoid from the Lower Coal Measures, of which the calyx is unfortunately wanting. When its characters are made known by future discoveries, I shall expect to find it with an anal side of the Taxocrinus type.

Notwithstanding the evident distinctness of the two plans, their early divergence from a common origin which can with reasonable probability be inferred, and their long duration as independent lines of structure, it is nevertheless a curious fact that they also tend to run together, in a sort of convergent evolution, toward the close of their history. I can show most beautifully by actual specimens how this has occurred in the Carboniferous between *Forbesiocrinus* and *Taxocrinus*, not so much in the way of individual variations as in the modification of species. We have a species of *Forbesiocrinus* in the Keokuk Limestone with a firmly plated anal area, in which there is a well-marked vertical series imbedded in the middle, but usually

tending toward the right. On the other hand, there is in the same formation, and at apparently the same horizon, a form of *Taxocrinus* in which, while the anal series is rounded and prominent, and merges plainly into the perisome above, the plates of the bordering integument, though still pliant, are strong and heavy, and apparently united to the adjacent brachials by loose suture. In these the modification begun in the last case has evidently been carried to a phase in which the strong structures composing the *Forbesiocrinus* plan have broken down in the anal area, and given place to the opposite one. It thus happens that we are sometimes in doubt to which of the two genera a species ought to be referred; and much of the confusion and shifting of opinion as to the relations of these genera is traceable to the failure to take proper account of these transition forms.

There was thus a sort of struggle for existence between the two plans, and it would seem that the group adhered in the end to that structure which was in best accord with its flexible characteristics; and we may perhaps infer that the Sagenocrinus plan, which tended more in the direction of the Camerate structure, was finally extinguished by reversion to the other one. This was fully accomplished in the Kaskaskia, where there is a species described by Hall as *Forbesiocrinus whitfieldi*,[1] and better illustrated by Miller and Gurley under the name *Taxocrinus wetherbyi*;[2] and of which Wetherby's *Forbesiocrinus parvus*[3] is a young individual—which has the habitus of the highest-developed *Forbesiocrinus* in everything except the anal side, where it is a perfect example of structure No. 1. In fact, the general character of the *Taxocrini* in the St. Louis and Kaskaskia Limestones is that of a strong interbrachial structure in the regular areas, combined with a weak and flexible one in the anal area, containing the conspicuous tube and its bordering integument.

In the first family—Ichthyocrinidae—structure No. 2, in its earlier stages, was the prevailing type, viz., one large plate, with perhaps the addition of a few smaller ones above it, completely filling the area. *Parichthyocrinus* alone of the genera hitherto assigned to the Ichthyo-

[1] *Geological Survey of Iowa*, Part II, p. 632.

[2] *Bulletin No. 6*, Illinois State Museum, Plate 4, Fig. 3.

[3] *Journal of the Cincinnati Society of Natural History*, Vol. II, Plate II, Figs. 4*a*–*b*.

crinidae, has the Taxocrinus anal structure thoroughly developed. Only its habitus of closely abutting arms differentiates it from *Taxocrinus*, and it must therefore be considered simply as a somewhat abrupt transition form from the Taxocrinidae toward the Ichthyocrinidae, or *vice versa*. But it is most interesting to note that in certain forms referred to *Lecanocrinus* we can almost see the transition actually going on, in the same horizon and locality. In *L. macropetalus*, from the Niagara group at Lockport, N. Y., we have a most characteristic example of the first family—a rounded, ovoid crown, with a perfectly even surface, with rays and arms flat dorsally and in close contact throughout (Plate VI, Figs. 13, 14). It has a single very large anal plate rising above the level of the radials, and curving to a point between the rays, which abut upon it at either side and close over it in an arch. This plate is without depressions of any kind, and is perfectly flush with the general curvature of the crown. In certain other species from the same locality and horizon, this plate begins to be depressed at the sides from the upper end down, so as to leave a ridgelike elevation in the middle, quite resembling the base of our so-called anal tube, while the full dimensions of the plate are still retained. In some specimens of these forms we can see this median ridge continued by a second small rounded plate, of the same form and size, the large anal having lost its pointed angle and become truncate to support this new plate. Here we have the beginning of our armlike anal series. If the process is pushed a little further, so that the depressed lateral margins of the large anal plate become replaced by perisome, we shall have a complete Taxocrinus anal side, and our *Lecanocrinus* will have been transformed into a *Gnorimocrinus*. It is now very curious that the tendency is actually in this direction as to those other characters on which the two families have been separated; for along with these changes in the anal plate there appear marked depressions between the rays and their divisions, which become rounded, with strong tendency to divergence in the upper portions, and to long and delicate arms. Hall's *Lecanocrinus ornatus*,[1] and Ringueberg's *L. nitidus*, *L. incisus*, and *L. excavatus*,[2] are forms in which this interesting modification occurs. I have de-

[1] *Palæontology of New York*, Vol II, Plate 44, Figs. *2a–m*.

[2] *Bulletin*, Buffalo Society of Natural History, Vol. V, Plate 1, Figs. 5, 6, and 7.

scribed this as a modification from *Lecanocrinus* toward *Gnorimocrinus*. Of course, we do not know which way it really was, and it is quite possible that the process of modification was in the opposite direction.

Which of these two plans was the primitive one we cannot determine from their paleontological history, as they both doubtless run far back into the obscurity of pre-Silurian epochs. The earliest known species of undoubted Flexibilia type—*Taxocrinus elegans* and *T. laevis* from the Trenton Limestone—I believe to have the Taxocrinus anal side;[1] and, on the other hand, *Cleiocrinus*, from the same horizon, which is at least a transition form with some flexible characteristics, has the opposite anal plan. There is, however, to be considered the question whether the morphological differences which gave rise to this structure have not continued to the present time in the Flexibilia Pinnata; and we may, in that connection, venture an opinion as to their probable origin.

The modifications in the external form of the calyx were undoubtedly due to differences in the position of the anus. If the gut issued from the visceral mass laterally, and remained there, the growing skeleton would be affected by its position, even to the extent of simulating its outline; and the lower down it issued, the more pronounced would be the separation of the rays by the tubelike structure. If it issued ventrally, and from the center of the disk, the skeleton would not be influenced by it at all, but should have perfect pentamerous symmetry. Between these two extremes we should have a wide range of variation in the outward form and arrangement of the anal side. And we may suppose that, as it shifted from a very low, lateral position, toward the margin of the disk, the tubelike row of plates would gradually disappear, or lose its identity by becoming incorporated in plates suturally united to the rays, like those of the regular interbrachial areas. By the time it had shifted well into the central part of the disk, all anal plates would be eliminated from the skeleton. Or the shifting might have taken place in the opposite direction, and the order of the changes in the skeleton have been reversed accordingly; although the first is more in accordance with

[1] This supposition is confirmed by the discovery of specimens since the above was written.

the observed facts. Such shifting in the position of the rectum is a fact well known in the embryology of the Echinoderms;[1] and it may be remarked that there are instances, both among the Camerata and the Inadunata, where the anus passed out through the test below the level of the arm-bases.

Fortunately for the purpose of our comparison, the only Crinoid whose embryology we know belongs to the Flexibilia. It has been the subject of elaborate and splendid researches by several distinguished and able investigators. The course of development of the anal plate in the larva of *Antedon*, as brought out by the works of these eminent men, lends force to the above suggestion.

Sir Wyville Thomson's account[2] of it is as follows:

> About the period of the development of the second radials, a forked spicule makes its appearance in one of the interradial spaces between the upper portion of two of the first brachial plates. This gradually extends in the usual way till it becomes developed into a round, cribriform, superficial plate. Simultaneously with the appearance of this "anal" plate, a cæcal process like the finger of a glove rises from one side of the stomach and curves toward the plate. The plate increases in size, becomes inclosed in a little flattened tubercle of sarcode, and maintaining its upright position it passes slightly outwards, leaving a space on the edge of the disk between itself and the base of the oral plate immediately within it. Toward this space the cæcal intestinal process directs itself. It rises up through it in the form of an elongated tubular closed papilla. The summit of the papilla is finally absorbed, and a patent anal opening is formed.

Dr. W. B. Carpenter continued the researches begun by Sir Wyville upon the development of *Antedon rosaceus*, and he has given,[3] with most admirable illustrations, the complete history of the anal plate. For the convenience of readers who may not happen to have this work at hand, I reproduce a few of his figures—some on a different scale of enlargement—which will assist me in explaining the thought I have in mind. In quoting some parts of Carpenter's description, I refer to the figures on my own plate instead of to his original numbers. He gives the following statement of the first appearance and subsequent history of this plate (p. 727):

[1] Bury on "Early Stages in the Development of *Antedon rosacea*," *Philosophical Transactions*, 1888 B, p. 294.

[2] "On the Embryology of *Antedon rosaceus*," *Philosophical Transactions*, 1865, p. 529.

[3] *Philosophical Transactions*, 1866, pp. 671 ff.

> Between two of the radials, and at the same level with them, an unsymmetrical plate early shows itself, the subsequent relation of which to the vent proves it to be an *anal* plate (Plate V, Fig. 4). . . . . Simultaneously with the appearance of the anal plate, a slender digitate process arises from one side of the stomach, and curves toward that plate: this constitutes the rudiment of the Intestine.

This is at a very early stage. At a little more advanced stage, shown by Figs. 5 and 6, Plate V, the account proceeds:

> The single anal plate originally interposed between two of the first radials (R. R.), being attached not so much to the neighboring plates as to the visceral mass, begins to be lifted out (as it were) from between them with the development of the anal funnel; and the space left by it is partly filled up by the lateral extension of the two radials between which it was previously interposed, but which do not yet come into complete contact (p. 732).

At a still later stage:

> The anal funnel (Plate V, Fig. 6) is now a very conspicuous object, the anal plate (x) which it bears on its outer side being altogether lifted out from between the two first radials which it originally separated (p. 734).

The anal plate finally disappears altogether before the adult stage is reached, and the anus takes up its permanent position toward the margin of the disk.

Thus we see that the position and movements of the anal plate are not governed by its connection with other plates of the aboral side, but that they depend upon the shifting and development of the gut, to which it is at an early stage attached. And we can readily trace, in the movements of the plate thus indicated, striking analogies to some of the anal conditions observed among the paleozoic genera.

Now we have, in the two great living genera of the Flexibilia Pinnata, just such differences in the position of the anus—though in less degree—as we have supposed to occur among the ancient forms; viz., that of *Antedon* being excentric, while that of *Actinometra*, alone of all known living Crinoids, is absolutely central. The excentricity of *Antedon*, while producing an anal plate in the larval skeleton, is not sufficient, or sufficiently persistent, to affect the form of the calyx in the adult, which in both genera has perfect pentamerous symmetry. It may be, therefore, that we have in these living genera a reminiscence of the long struggle among their paleozoic antecedents between these opposing tendencies.

We may also be warranted in supposing, from the observed course of development of the anal structures in the larva of *Antedon* as above described, that the Taxocrinus plan represents the earliest and most primitive form, and that the modifications of this in paleontological time were those which tended toward the disappearance of the row of anal plates, with its border of perisome, and the substitution of regular calyx plates, suturally connected with the adjacent rays. Hence the outcome of the struggle in paleozoic time was the survival of the original plan, and the suppression of the modified one.

3. The third modification of the anal structures, which also runs from the Silurian to the Carboniferous, is that in which the anal plate has altogether disappeared, and it is merely a further extension of one of the preceding. This occurred in the Silurian in the genus *Ichthyocrinus*, while still retaining its primitive radianal, which it did not get rid of until the Carboniferous, where, in the genus *Metichthyocrinus*, we have a Crinoid with perfect pentamerous symmetry, so far as the external test shows. Two genera in the division with divergent arms reach this stage also in the Carboniferous—*Wachsmuthicrinus*, in which traces of bilateral symmetry can be seen in the slightly larger size of the posterior basal, and *Nipterocrinus*, in which the pentamerous symmetry seems to be perfect. This modification apparently did not much influence the history of the group.

c) The first modification in the brachial system—i. e., in the number of primibrachs—has already been described and discussed as to its details. There can be little question that the primitive form in this respect was that with two primibrachs. It belongs to the *Antedon* larva, and it prevailed almost exclusively in the Silurian. The few cases in which there is but one primibrach may be explained by the syzygial union of two of the primitive brachials, just as happens in some species of the living *Antedon*, without changing the fundamental plan. The addition of another primary brachial simultaneously in all of the rays, producing the 3-IBr structure, cannot be explained in any such way, and the occurrence of this form in the Silurian is so limited and exceptional that it may scarcely be said to have had a beginning before the Devonian. It is clearly the successor of the first one, in the paleozoic. The two-IBr structure con-

tinued from the Silurian through the Devonian, and into the Carboniferous, with constantly diminishing importance, ending, so far as known, in the Keokuk Limestone; but reappearing with the Flexibilia Pinnata in the Mesozoic, and continuing to the present time. The three-IBr structure, on the other hand, having barely made a beginning in the Silurian, shows a steady increase through the Devonian and Carboniferous, and prevailed exclusively in the Warsaw, St. Louis, and Kaskaskia, in the genera *Forbesiocrinus*, *Taxocrinus*, and *Onychocrinus*, with a slight tendency in *Taxocrinus* of the Kaskaskia, to reversion to the original form. Therefore this is not a case of parallel development, but is that of the suppression of the earlier structure, and its replacement by the later one, which disappeared only with the extinction of the nonpinnulate division of the Flexibilia toward the close of the Carboniferous. In the latest and most extravagant genus of the group, *Onychocrinus*, it shows a tendency to further development by the addition of another brachial, not sporadically, but constantly, as a well-defined character among species. From the tenacious grip that this structure had upon several of the strongest genera, it must be regarded as a morphological change of much importance, strongly affecting the phylogenetic history of the group; but yet subordinate, in my opinion, to the great differentiation of the anal structure, and therefore not available for defining large divisions.

The second brachial modification is marked by interesting changes in the mode of branching of the rays above the first axillary from a more or less regular division of the rays by successive bifurcations—dichotomy—to one into large main branches, or arm-trunks, bearing ramules on one or both sides—heterotomy. Both were established in the Silurian, and continued through the Devonian and Carboniferous, and were in force, side by side, in the genera *Taxocrinus* and *Onychocrinus*, at the close of the Subcarboniferous in the Kaskaskia. The dichotomous plan, which was probably the primitive one, was by far the most prevalent throughout; and the heterotomous plan was a modification which, while it ran parallel to the other until the end of the group, did not supplant it. The differences arising out of this modification afford very good characters for generic distinction.

d) The modification in the plates of the interbrachial areas might properly have been considered in connection with those of the anal side, inasmuch as they all belong to the system of supplementary plates, as distinguished from that to which the brachials belong. Sir Wyville Thomson was led by his researches on the embryology of *Antedon*[1] to regard the skeleton of the Crinoid as composed of two systems of plates, which he states to be thoroughly distinct in their structure and mode of growth. These he designated as the *Radial*, and the *Perisomatic*, systems of plates. The former are distinguished by being chiefly made up of peculiar fasciculated tissue of parallel rods, while the latter commence as simple cribriform films embedded in the outer layer of the perisome, and thicken by a repetition inwards of the same diffuse areolar tissue. The Radial system he considers to include the joints of the stem, the centrodorsal plate, the radial plates, and the plates of the arms and pinnules, or brachials. To the Perisomatic system he refers the basal and oral plates, the anal plate, the interradial plates sometimes seen between the second radials, and any other plates or spicules that may be developed in the perisome of the cup or disk. Dr. Carpenter,[2] while not agreeing altogether with Sir Wyville as to the grounds of differentiation of these plates, substantially recognizes the two systems of radial and perisomatic plates as defined by him, except that he ranks the basal plates with the former instead of the latter.

Wachsmuth and Springer[3] divided the plates of the Crinoid skeleton into *primary* and *supplementary* plates; the former including the stem joints, infrabasals, basals, radials, brachials, orals, and ambulacrals, and the latter the anal, interbrachial, and interambulacral plates. According to either of these groupings of the plates, the anals and interbrachials fall under the same category. It was also demonstrated by Wachsmuth and Springer[4] that all plates interposed between the rays, from the basals to the orals, whether interbrachial or interambulacral, belong morphologically to the same ele-

[1] *Philosophical Transactions*, 1865, p. 540.

[2] *Ibid.*, 1866, p. 742.

[3] *North American Crinoidea Camerata*, pp. 38–105.

[4] "The Perisomic Plates of the Crinoids," *Proceedings*, Academy of Science, Philadelphia, 1892, pp. 345–75.

ment. Hence it follows that, if in the growing Crinoid certain spicules of the ventral perisome developed into well-defined plates, which remained permanently in a definite position in the axils between the radials or brachials, they would become the interbrachial (or interradial) plates as we know them; so that whether a certain form has interbrachials or not depends upon the extent to which the perisome developed downward into the axils.

Some traces of the development of this element are to be found in the *Antedon* larva. Sir Wyvill Thomson[1] thus describes their occurrence:

> In one or two cases I have observed about the time of the first appearance of the anal plate a series of five minute rounded plates, developed interradially between the lower edges of the oral plates and the upper edges of the basals. These interradial plates sometimes remain permanent in the mature *Antedon rosaceus*, and they appear to be constantly present in some species, as for instance in another and rarer British form, *A. milleri*. They usually occur, finally, in groups of three or five. They are irregular in form, and they resemble the anal plate in structure and mode of growth.

Dr. Carpenter figures two clusters of these plates, as seen at the inside of the calyx;[2] and J. S. Miller shows one such plate in each axil of his *Comatula fimbriata*,[3] which he calls "intercostal plates or joints." These observations of the so-called interradial plates in *Antedon* have been rather discredited by some subsequent authors in the course of controversial discussions, but I see no reason for questioning them. The occurrences as described seem to me entirely in harmony with the morphology of the group, and if they had not already been seen, I should confidently expect them to be found by further research.

It is evident from Dr. Carpenter's figure that these plates are more conspicuous on the interior of the young *Antedon* than at the exterior; in other words, that the growth is from within outwards. This accords very well with the observed facts among the fossils of this group. I have many specimens showing how the interbrachial plates diminish in size and number from the interior of the calyx to the exterior. In many cases where they are well developed on the

[1] *Op. cit.*, p. 540.

[2] *Philosophical Transactions*, 1866, Plate 39, Fig. 7.

[3] *Natural History of the Crinoidea*, Frontispiece, Fig. 2, G.

inside they appear as mere points at the outer surface, and often they do not pass through the wall; so that in a given interradius we may count twice as many plates interiorly as exteriorly. In some genera which are usually without any such plates, a straggling one is occasionally seen, and it is quite probable that, if we could see the interior of all the specimens, we should find many instances of such plates which have not come to the surface. It is a fact thoroughly established that these plates multiply with the growth of the individual; but it would seem that in those forms in which the rays are more or less contiguous, and tend to arch over the interbrachial areas, the plates are crowded by the growth of brachials, and to a certain extent reduced or suppressed at the outer surface of the calyx. In genera like *Taxocrinus*, *Forbesiocrinus*, and *Uintacrinus* the variance of the interbrachials with age is very marked, young individuals in some species having none at all, while the adults are profusely supplied. In *Wachsmuthicrinus*, which has no anal plate, the interbrachials are still more variable, being present or absent in the adult of the same species. In *Nipterocrinus*, and probably in *Pycnosaccus*, and the form described by Angelin as *Forbesiocrinus obesus*, the perisome extended down to the radials as a plated integument, without developing any well-defined interbrachial plates.

Notwithstanding the irregularities in some cases above mentioned, the varying development of the interbrachial plates affords important characters for classification in this group. In some genera the perisome did not extend down between the rays in such a manner as to form any permanent plates in the interbrachial areas; in others they were abundantly developed. Both forms extend from the Silurian to the Carboniferous; the first being characteristic of a little group of genera which may be taken as the typical Ichthyocrinidae, and correlating with another character to be mentioned presently. The tendency in the paleontological history of the group generally is the same as in the individual, viz., toward an increase in interbrachials. But few forms without such plates are found after the Silurian, while in the Carboniferous their presence in considerable numbers is the general rule. Nevertheless, the latter stage was fully attained in the Silurian in the genus *Sagenocrinus*.

There is another modification, not suggested by anything apparent in the primitive type, but affecting the general form and habitus of these Crinoids in a way that is of considerable practical importance. Anyone who has had occasion to arrange the fossils of this group cannot help being struck by the presence of two general types. One is marked by a tendency of the calyx and arms to form a globose, ovoid, or pyriform crown, in which the arms lie in close contact—although in some genera the lower part of the rays are separated by wide interbrachial areas, above which they come together again. In the other, on the contrary, the tendency is toward a spreading crown, caused by the increasing divergence of the rays upward. In the first the plates of the rays and arms, and the intervening interbrachial structures when present, are for a considerable distance up more or less flush with one another exteriorly, so that the general curvature of the crown is but little interrupted. In the second, the rays and their divisions are rounded exteriorly, and the interbrachial spaces relatively depressed, so as to emphasize the appearance of divergence above alluded to.

Between such forms as *Ichthyocrinus* or *Lecanocrinus* on the one hand, and *Taxocrinus* or *Onychocrinus* on the other, there is not the slightest difficulty in distinguishing by the above character. But there are occasional species, otherwise characteristic of the first group which are pretty deeply furrowed between the rays and arms, and some of the second whose arms are habitually rather closely packed together, which we could not so readily assign to their respective groups, except for their evident connection with related genera whose characteristic species fall within them without any trouble. On the other hand, there are a few forms which we are inclined to transfer from the group which they superficially resemble, because of some peculiar association of other characters which indicate a probable closer relationship elsewhere.

Now, I confess myself unable to point out any satisfactory morphological basis for the difference in habitus between these two divisions, and I have much doubt as to its structural importance. Yet it is so constant and well marked in many cases, and affords such a palpable and convenient means of separation in this perplexing group, that we find it of some use in our classifications. It formed

a rather too prominent basis of my former arrangement. Both forms existed in the Lower Silurian, and continued into the Carboniferous; the first one greatly diminished and ending in the Keokuk Limestone, with a single exception—probably a transition form—in the Coal Measures; and the second continuing with increasing importance to the end of the Subcarboniferous. The first division comprises a little group of rare genera, mostly confined to the Silurian, but with evident descendants in the Devonian and Carboniferous. They are mostly small, *Ichthyocrinus* alone occasionally attaining a considerable size. In the number of primibrachs and the absence of interbrachials they fall together nicely, and in the structure of the anal side they represent, for the most part, an earlier stage of development of the *Sagenocrinus* plan than those of the other division. The second division, with the divergent arms, embraces genera of both forms of brachial modification, and also the two leading types of anal structure. It appeared in the Silurian, and steadily increased to the close of the Kaskaskia, where it is represented by its most conspicuous example, *Onychocrinus.*

It is evident that most of the modifications above considered have influenced the line of succession from the primitive type of this group, and its separation into subordinate divisions. Each one of them is doubtless a factor entering into the classification that nature has made—though of very different values—and the probability is that every natural division which has been produced is a composite product, the resultant of the interaction of two or more of these tendencies to modification upon independent lines. Just how much influence each has had in fixing the line of succession we have no means of determining. It is possible to arrange the genera upon the basis of either one of the leading morphological changes I have mentioned; but whichever is selected for this purpose, we find our arrangement more or less disturbed by some of the others. For example, a fairly satisfactory arrangement could be based upon the modification of the primary brachials, which would correlate quite well with other characters, if it were not for the fact that this would throw *Sagenocrinus* and *Forbesiocrinus* into different families; whereas the connection betewen these genera is so evident, and the line of descent

so probable, that we cannot feel like accepting any scheme which compels their separation. We cannot, of course, represent lines of descent in space of two dimensions, so that anything in the way of a diagram or table would be imperfect, even if we knew all the facts. Still less is it practicable when many of the relationships rest wholly in conjecture.

In some groups of the Crinoids family divisions are most sharply marked. No one need ever be in doubt, from inspection of the calyx alone, whether a Camerate Crinoid belongs to the Rhodocrinidae, Melocrinidae, Actinocrinidae, Batocrinidae, Platycrinidae, or Hexacrinidae. This cannot be said of the Flexibilia. By reason of the fundamental difference in construction of the two groups, there is not in the latter that sharp demarkation between calyx and arms which is so characteristic of most of the Camerata. Here, on the contrary, in by far the greater number of the genera, the calyx passes into the arms by imperceptible gradation, so that in the fossil state, being usually unable to see any part of the tegmen, we cannot tell with certainty where the calyx ends and the arms begin. The different modifications of this structure also shade into one another by various transitions, which is the reason why groups of family rank may be formed, as above stated, which differ somewhat according to the character which is taken as the basis of division.

Nevertheless, it seems possible to form a reasonable opinion as to the relative importance of the characters, as the basis for large divisions:

1. The differentiation of the anal area, being found completely developed in the earliest Silurian, and continuous almost to the end of its history, may be taken as marking the most primitive division of the group. It evidently dominated the lines of descent throughout, and should therefore be accorded first importance in the definition of families, all others being subordinate modifications, affecting one or the other of these lines, but probably not interrupting them.

2. The presence or absence of interbrachials affords a useful basis of subordinate divisions.

3. The differentiation of the brachial system in the number of primary brachials, although evidently affording characters of much importance, is one which has impressed itself with varying force

upon the two primitive lines, and not in a parallel progression. It may be assumed to be a subordinate modification, marking the limitations of genera, and perhaps of sub-family divisions.

4. The difference in general form and habitus, while not explainable upon any known morphological ground, and therefore with our present knowledge apparently of less value than either of the foregoing, nevertheless furnishes a ground for division which is of some practical importance in the construction of a table, and it may therefore be given a rank in our classification perhaps higher than it at present logically deserves.

The other modifications are so palpably limited in their effect upon the history of the group that they need not be considered except in the separation of genera. I do not believe that the higher arm structure is a good character for the definition of families. It appears in parallel successions in other groups of the Crinoids, where it is most interesting in the development from more or less equal branching to radial extensions in the form of main arm-trunks or branches bearing subordinate ramules. This is conspicuously shown among the Camerata in several of the best defined families, viz., in the Rhodocrinidae from *Rhodocrinus* to *Ripidocrinus;* in the Melocrinidae from *Glyptocrinus* to *Melocrinus;* in the Actinocrinidae from *Actinocrinus* to *Steganocrinus;* in the Platycrinidae from *Platycrinus* to *Eucladocrinus;* and in the Hexacrinidae from *Arthracantha* to *Hexacrinus.* Yet there can be no thought of questioning the arrangement of these beautifully defined families on account of these arm characters, or of contending that they represent anything more than a minor variation.

The arrangement of which I am at present in search is one for practical utility, that will facilitate the study of this group; and I am not attempting to express fully the phylogenetic relations of the various forms even as I might conceive them to be, although I have tried to recognize some of the evident lines of descent. Taking as a basis the primitive differentiation of the anal system, the Flexibilia Impinnata may be divided into two groups, and the first of these may be again divided upon the interbrachial system and the general form and habitus. This will give three main divisions, A, B, and C; of which A and B will agree with each other and differ from C in

the anal structure, while they will differ from each other in the interbrachials, and partly in the form. In this way the known genera of this group—with the exception of some transition forms whose place is difficult to assign—will fall into three principal family divisions, which differ from each other in various degrees, according as one or the other character is given the greater importance. Each of them contains further groupings of genera upon some of the other characters, which might be given subordinate designations according to our notions of their value.

This might be considered an imperfect attempt to work out the resultant of the several modifications which I have mentioned, and it necessarily encounters difficulties which can be evaded only by some arbitrary—and perhaps temporary—disposition of the disturbing elements. As to these no scheme will ever be perfectly satisfactory, and there will always be some shifting of opinion by different observers, and even by the same observer from different points of view. For instance, as to some of the characters, we cannot always give them the same order of precedence in the tables. If we had genera showing every possible combination of the modifications we have discussed, it might be practicable to construct a table with some uniform order of sequence. We do not, however, find all such combinations, and it is quite conceivable that they were never all accomplished. But it is also to be confidently expected that some additional ones will yet come to light, and we can readily point out some vacancies to be filled by future discoveries.

These three families are not so very different from those heretofore proposed, although the grounds upon which they are defined are considerably changed. In my former paper, above cited, I arranged the genera into two main family groups, based upon the difference in the habitus and general form; and I stated that the second family might perhaps be divided into two subgroups. There is no very material difference in the general arangement I now propose, except that I carry this suggestion a step farther, and erect the two subgroups into families of equal rank with the first, thus bringing in an additional family—Sagenocrinidae—between the other two; while also restricting the first group within somewhat narrower limits.

The definitions of a number of the genera differ considerably

from those given by Wachsmuth and Springer in the *Revision oj the Palaeocrinidae*, Part I. Discovery and research since that time have greatly added to our information touching this group, which was then by no means well understood. In *Gnorimocrinus* the typical species is *G. expansus* Ang.,[1] and several of the species listed under this genus in the *Revision* are now found to belong to other genera. For instance, *G. excavatus* Schultze doubtless belongs to *Dactylocrinus;* and perhaps *G. oblongatus* and *G. rigens* also. *G. ovalis, salteri, interbrachiatus*, and *austini* I have referred to a new genus, *Protaxocrinus;* while *G. loveni*, by reason of its possession of three primibrachs, and a radianal in addition under the right posterior ray, will form the type of another new genus, for which I propose the name *Meristocrinus*.

In *Lithocrinus* the typical species is *L. divaricatus* Ang. (including *L. robustus* syn),[2] which has no radianal; while for *L. obesus*, which has a radianal, and apparently a different interbrachial structure, I have found it necessary to propose a new genus, *Cholocrinus*.

Under *Onychocrinus* there are two well-marked types, represented by *O. ramulosus* and *O. exsculptus*, which probably might be separated generically. The first has three primibrachs, and the latter four; and besides this, the habitus of the two species is so distinct that they can be recognized from the smallest fragments. The *exsculptus* type runs from the Burlington to the St. Louis, and probably to the Kaskaskia, and the *ramulosus* type from the Keokuk to the Kaskaskia.

In like manner, I think it probable that *Forbesiocrinus agassizi* with its two primibrachs, should be separated from the other species of the genus, which all have three. In fact, the analysis of the genera indicates the definition of other new genera which will have to be proposed, in order to cover cases already known or hereafter to be discovered.

The analysis of the Flexibilia genera here given is an improvement upon the former one, resulting from the foregoing observations. In considering any such arrangement, reasonable latitude must be allowed in construing descriptive terms, which cannot be made to fit all cases by any hard and fast lines. It must not be forgotten

[1] *Iconographia Crinoideorum*, Plate XX, Figs. 15, 16.

[2] *Ibid.*, Plate XXI, Figs. 11, 12, 21.

that the most important characters often shade into one another to a greater or less degree. For instance, in speaking of the arm-branching, we cannot confine the term "dichotomous" to such symmetrically dividing rays as are found in *Cyathocrinus;* but it must be taken to mean simply that the rays divide by a more or less regular bifurcation, as opposed to those in which the branches are given off in the form of lateral ramules markedly smaller than the main trunk, as in *Onychocrinus*, which we call "heterotomous." So as to whether the arms are contiguous or divergent, the terms are relative and not absolute; and while, as in other characters, the extremes are well marked, the two plans of arm arrangement sometimes approach each other so closely that all we can say in some genera is that the tendency is in one direction rather than the other. In the matter of interbrachials, there are really two kinds of plates: the regular, strong plates that occur in the axils, and the small irregular plates or granules forming the pliant integument which extends from the tegmen, in varying degrees, and for varying distances, down between the rays and their divisions. When in the descriptions we speak of "IBr plates," we mean the former.

It must also be remembered that it is impossible in any such scheme to represent the exact degree of relationship of genera, even as we understand it to be. We necessarily grade our divisions according to the greater or less generality of the characters; and we find in some cases that this will throw into different larger groups two genera that we should upon other grounds place next to each other.

Bearing in mind these qualifications, the following analysis may be found fairly practical, according to our present knowledge:

ANALYSIS OF THE GENERA

I. Anal plates, when present, incorporated in calyx by sutural union with adjacent rays.
  - A. Rays in contact all around, or separated only at anal side; arms contiguous . . . . ICHTHYOCRINIDAE
    - *a.* Radianal.
      - i. RA under r. post. R.
        - Primibrachs 2.
          - Arms dichotomous.
            - Anal x alone, or followed by others . . . . *Clidochirus*
            - No anals . . . . *Ichthyocrinus*
          - Arms heterotomous . . . .

ii. RA rhomboidal, obliquely to left of r. post. R.
Primibrachs 2 (exceptionally I).
Arms dichotomous; IBr 2 or 1.
Anal x alone, or followed by others in series. . *Lecanocrinus* (Cyrtidocrinus)

b. No radianal.
Primibrachs 2.
Arms dichotomous.
Anal x with triangular plate above; arms with dextrorse twist . . . . *Mespilocrinus*

c. No anal nor radianal.
Primibrachs 2.
Arms dichotomous . . . . *Metichthyocrinus*
Primibrachs 3.
Arms dichotomous.
(Anal side unknown, but from form of calyx probably not distinct) . . . . (*I. greenei*) . . . .

B. Rays separated all around by interbrachial plates SAGENOCRINIDAE
a. Radianal.
1. Anal area more or less completely filled by solid plates, forming part of calyx wall.
i. Large anal x alone, or followed by others in single series.
Arms more or less contiguous.
Primibrachs 2 or less.
RA more or less under r. post. R., above the line of BB; iBr few.
Arms dichotomous . . . . *Anisocrinus*
Arms heterotomous . . . .
RA variable, either between BB or absent.
Infrabasals very large, enveloping BB.
Arms dichotomous with ramules inside dichotom; iBr few.
10 main arm-trunks; RA generally present . . . . *Homalocrinus*
20 main arm-trunks; RA generally absent . . . . *Calpiocrinus*
Arms more or less divergent.
RA rhomboidal, obliquely to left of r. post. R.
Arms dichotomous; IBr generally 1.
iBr areas wide, occupied by small, irregular plates; IBr not filling distal face of RR *Pycnosacus*
Arms heterotomous; 10 main arm-trunks with ramules inside dichotom; iBr areas wide; IBr not filling distal face of RR.
(L. obesus n. g.) *Cholocrinus*

ii. Anals numerous, in more than one series.
Arms more or less divergent.
Primibachs 2.
RA more or less between BB.
Arms dichotomous; iBr numerous . *Sagenocrinus*

2. Anal x and smaller plates occupying only lower part of anal area.
i. Anals in more than one series.
Arms more or less divergent.
Primibrachs 2.
RA under r. post. R., above line of BB.
Arm dichotomous; iBr few . . . *Temnocrinus*

b. No radianal.
1. Anal x and smaller plates occupying lower part of anal area.
i. Anals few, mostly confined to single series.
Arms more or less divergent.
Primibrachs 2.
Arms dichotomous.
IBr areas wide; IBr not filling distal face of RR . . . .
Arms heterotomous.
10 main arm-trunks with ramules inside dichotom; IBr few . . . . *Dactylocrinus*
Arms more or less contiguous.
Primibrachs 2.
Arms dichotomous; iBr numerous (n. g.) *Amphicrinus*
Primibrachs 3.
Arms dichotomous; iBr few . . . *Euryocrinus*

2. Anal area filled by solid plates, forming part of calyx wall.
Anals numerous, in more than one series.
Arms more or less divergent.
Primibrachs 3 (exceptionally 2).
Arms heterotomous.
10 main arm-trunks with ramules inside dichotom.
iBr numerous . . . . *Lithocrinus*
Arms dichotomous
iBr numerous . . . . . *Forbesiocrinus*

c. No anals nor radianal.
Arms more or less divergent.
Arms heterotomous. Primibrachs, 2.
10 main arm-trunks with ramules inside dichotom

iBr variable or absent . *Wachsmuthicrinus*

Arms dichotomous; Primibrachs 3.

iBr areas wide; IBr not filling distal face of RR., and connected by integument of small plates.

IBB undivided . . . . *Nipterocrinus*

II. Anal plates, when present, not united by suture with adjacent rays, but in armlike series, more or less separated from them by perisome.

C. Arms generally divergent. . . . . TAXOCRINIDAE

a. Radianal.

i. RA under r. post. R.

Arms dichotomous; iBr few (*T. ovalis*, n.g.) *Protaxocrinus*

ii. RA obliquely to left of r. post. R.

Arms dichotomous; iBr few.

Primibrachs 2 . . . . *Gnorimocrinus*

Primibrachs 3 . . . (*T. loveni*, n. g.) *Meristocrinus*

b. No radianal.

i. Arms dichotomous; iBr variable.

Primibrachs 2 . . . (*T. affinis*, n. g.) *Eutaxocrinus*

Primibrachs 3 . . . . *Taxocrinus*

Arms contiguous . . . . . *Parichthyocrinus*

ii. Arms heterotomous; iBr variable.

20 main arm-trunks with ramules inside dichotom;

Primibrachs 2 . . . . *Synerocrinus*

10 main arm-trunks, with ramules.

Ramules unilateral, outside of dichotom;

Primibrachs 3 . . . . *Oligocrinus*

Ramules bilateral, branching in clusters on both sides of dichotom; Primibrachs 3 or more.

Onychocrinus

c. No anals nor radianal.

INTERMEDIATE FORMS OF UNCERTAIN PLACE

Between Flexibilia and Camerata.

Dicyclic; higher brachials incorporated in calyx by lateral union; calyx pliant, plates united by loose suture; pinnulate; IBB 5; IBr 2; no iBr except at anal side; anal plates in vertical succession, filling area and connected by suture with adjacent brachials . . *Cleiocrinus*

Between Flexibilia and Inadunata.

Dicyclic; 5 simple arms, free from radials up; except for small, irregular IBr of doubtful extent; habitus of *Symbathocrinus* . *Rhopalocrinus*

Base doubtful; arms dichotomous, branching many times; rays free from radials up, except for possible integument of small plates; anal side doubtful . . . . *Caleidocrinus*

EXPLANATION OF PLATE IV

Onychocrinus ulrichi M. and G.

Fig. 1.—The ventral disk or tegmen complete, except as to one ray, which is broken off; view from above, anterior side at the top. It shows the pyramid of four small orals at the center, two of them very plain, the third less so, and the fourth, at the left, pushed in under the others and invisible from this view; the large posterior oral with the ambulacra running along the sides, and the anal appendage bent over to the right under its posterior margin. The rows of ambulacral plates are seen extending from the oral pyramid to and along the rays, with the plated integument between them. The whole disk is now concave, having sunk down into the bottom of the calyx, and the view of the large posterior oral is somewhat foreshortened. The infolding ramules of the arms are well shown in two of the rays.

Fig. 2.—The disk of another specimen, seen from the under side—the calyx plates having been removed; posterior side up. This shows the same structures as Fig. 1, only viewed from the opposite side. The opening between the orals, and the undulating under surface of the posterior oral, are well shown; also the keeled inner surfaces of the ambulacrals.

Fig. 3.—Disk of another specimen, same view as in Fig. 1; showing the same structures, but with the curved anal appendage in plain view, and a portion of the plated integument, or perisome, attached to it at the right. The orals are much displaced, and the view of the posterior one greatly foreshortened; a row of strong plates proceeding from the shoulders of the posterior oral is well preserved in this specimen, perhaps serving as a brace for the tegmen.

Fig. 4.—Detail of central part of disk from another specimen; to show the perforate structure of the posterior oral. In order to get a better light on this plate, the specimen is drawn with posterior side up. This specimen shows but little aside from the posterior oral; the anterior orals are in position, in a more advanced stage of resorption than those in the other specimens; the round object at the right is probably a foreign body. The granules in the tegmen seem to be somewhat larger than usual. ×2.

Fig. 5.—Dorsal view of calyx and two complete rays, showing this aspect of the anal appendage.

Thaumatocrinus renovatus P. H. Carpenter

Fig. 6.—View of the disk from above; showing the oral pyramid, the marginal zone of small plates between the orals and the interradials, and the anal tube with its appendage of strong plates. The protuberances seen between the arm-bases are the interradials, which separate the radials all around. (After P. H. Carpenter, *Philosophical Transactions*, Plate 71, Fig. 5. ×15.)

(All figures except 4 natural size).

EXPLANATION OF PLATE V

Antedon rosaceus

Fig. 1.—Early Pentacrinoid larva, spirit specimen, with its tentacular apparatus retracted; showing basals, radials, and rudimentary primibrachs, and the orals opened out. (From W. B. Carpenter, Plate XXXIX, Fig. 1A. ×15.)

Fig. 2.—The same, at a somewhat later stage, spirit specimen; showing incipient

development of arms from the IBr, and the relative increase in size of radials; cirri not yet developed. (W. B. Carpenter, Plate XXXIX, Fig. 1B. ×15.)

FIG. 3.—Skeleton of early Pentacrinoid larva at a little later stage, dried specimen; showing the manner in which the calyx can be, at that stage, completely closed by the folding together of the orals, *o, o;* cirri beginning to appear. (W. B. Carpenter Plate XXXIX, Fig. 2. ×35.)

FIG. 4.—Skeleton of Pentacrinoid larva, same stage as Fig. 2, dried specimen; showing anal plate *x* between two radials, and resting on the posterior basal. (W. B. Carpenter, Plate XLI, Fig. I. ×30.)

FIG. 5.—Skeleton of Pentacrinoid larva, in still later stage; showing the anal plate *x* now being lifted up from between the radials; cirri well started. (W. B. Carpenter, Plate XXXIX, Fig. 3. ×25.)

FIG. 6.—Pentacrinoid larva at a still later stage, when almost ready to cast off the stem. The anal plate *x* detached from the radials (which are nearly closed beneath it), and lifted from between them by the development of the anal tube *a*, to which it is attached; centrodorsal and cirri well developed. (W. B. Carpenter, Plate XL, Fig. 2. ×30.)

FIG. 7.—Opposite view of the same specimen, with one ray removed to show the oral apparatus. The orals, *o, o*, now completely separated from the radials, and relatively carried inward by the development of the membranous perisome, *p*. (W. B. Carpenter, Plate XL, Fig. 1. ×30.)

HOLOPUS RANGEI

FIG. 8.—View of the disk, with closed orals, *o, o*, perforated; and small plates at base separating the orals from the radials. (From P. H. Carpenter, *Chall. Rep. St. Cr.*, Plate III, Fig. 2. ×$\frac{5}{2}$.)

FIG. 9.—Hypothetical figure of primitive Flexibilia calyx; with infrabasals, radianal, anal *x* between radials, and two primibrachs.

EXPLANATION OF PLATE VI

(On this and the following plate the radianal is shaded with vertical lines.)

ICHTHYOCRINUS Conrad

FIG. 1.—*I. laevis* Conr. Upper Silurian, Grimsby, Canada.

FIG. 2.—*I. subangularis* Hall. Upper Silurian, Waldron, Ind.

FIG. 3.—*I. pyriformis.* Upper Silurian, Dudley, England.

FIG. 4.—*I. pyriformis* (fide Angelin). ×2. Upper Silurian, Gotland, Sweden. From original to Angelin's XXII, 22.

FIG. 5.—*I. intermedius* Ang. ×2. Upper Silurian, Gotland, Sweden.

FIG. 6.—*I. gotlandicus* W. and Sp. ×2. Upper Silurian, Gotland, Sweden.

These figures all show the extra plate—radianal—at the base of the right posterior ray.

CLIDOCHIRUS Angelin

FIG. 7.—*C. pyrum* Ang. Upper Silurian, Gotland, Sweden. View from right posterior radius.

FIG. 8.—View from posterior interradius of another specimen—the original to Angelin, XVII, 6.

ANISOCRINUS Angelin

FIG. 9.—*A. interradiatus* Ang. Upper Silurian, Gotland, Sweden. Posterior, view; from original to Angelin, XXII, 18.

FIG. 10.—*A. angelini* W. and Sp. Upper Silurian, Gotland, Sweden. Posterior view. × 2.

FIG. 11.—*A. greenei* M. and G. sp. Upper Silurian, Louisville, Ky. Posterior view.

FIG. 12.—*A. oswegoensis* M. and G. sp. Upper Silurian, Oswego, Ill. Posterior view.

In all these the radianal is seen in primitive position directly below the right posterior ray.

LECANOCRINUS Hall

FIG. 13.—*L. macropetalus* Hall. Upper Silurian, Lockport, N. Y. Posterior view, showing radianal obliquely under right posterior radial.

FIG. 14.—*Ibid.* Anterior view of another specimen, to show absence of regular interbrachials.

METICHTHYOCRINUS n. g.

FIG. 15.—*M. burlingtonensis* Hall. L. Carboniferous, Burlington, Iowa. Without any radianal.

OLIGOCRINUS Springer

FIG. 16.—*O. asteriaeformis* Hall. L. Carboniferous, Burlington, Iowa. Anterior view of one of the type specimens; to show the mode of arm-branching.

PARICHTHYOCRINUS Springer.

FIG. 17.—*P. nobilis* W. and Sp. L. Carboniferous, Burlington, Iowa. Posterior view; anals in tubelike series.

NIPTEROCRINUS Wachsmuth

FIG. 18.—*N. wachsmuthi* M. and W. L. Carboniferous, Burlington, Iowa. Basal view; anal side not distinct; infrabasals probably coalesced.

WACHMUTHICRINUS Springer

FIG. 19.—*W. thiemei* Hall. L. Carboniferous, Burlington, Iowa. Basal view; no anal plates, but posterior basal in this specimen the largest.

(Figs. 4, 5, 6, 8, 9, and 11 after Liljevall.)

EXPLANATION OF PLATE VII

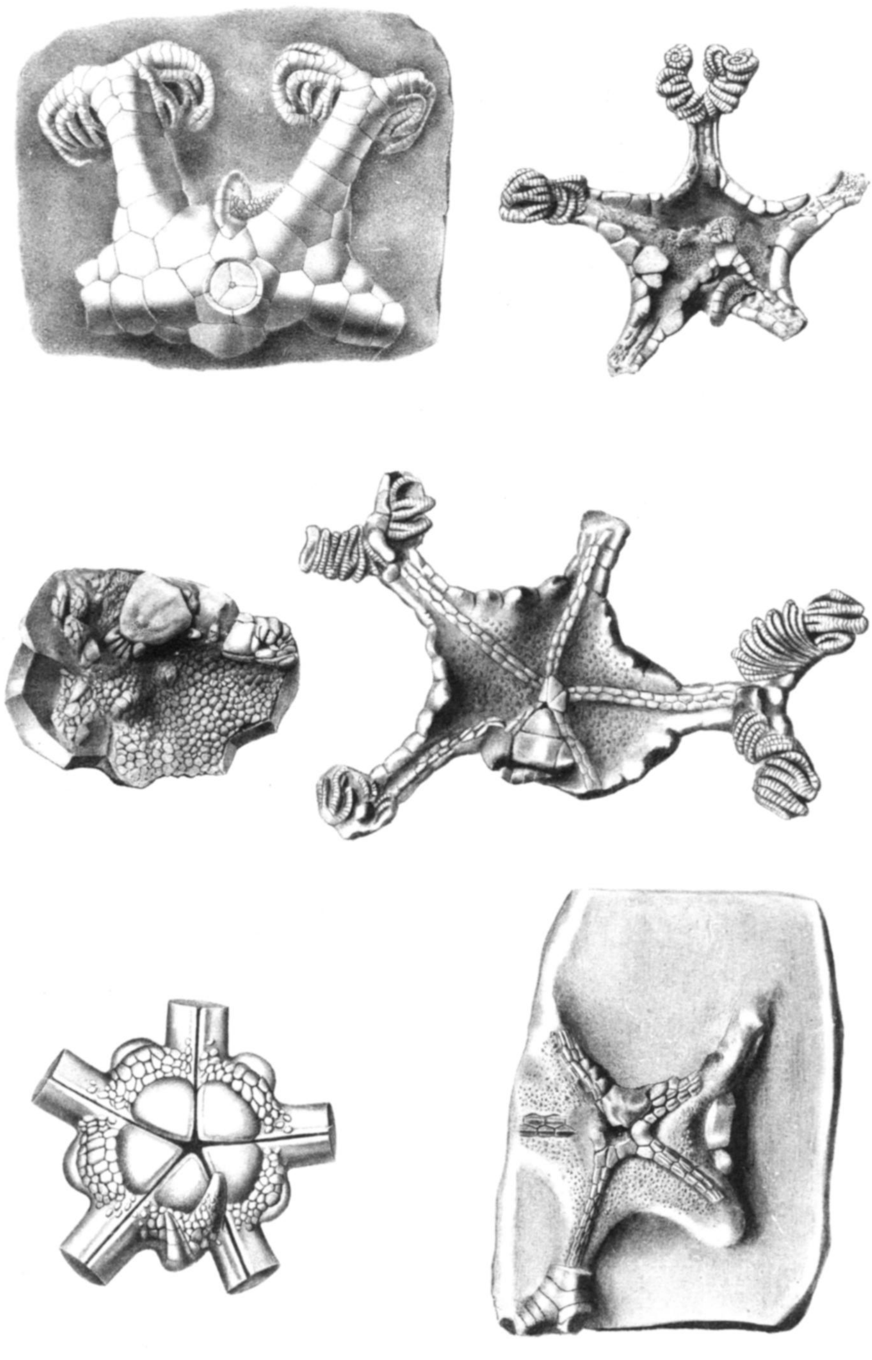
CALPIOCRINUS Angelin

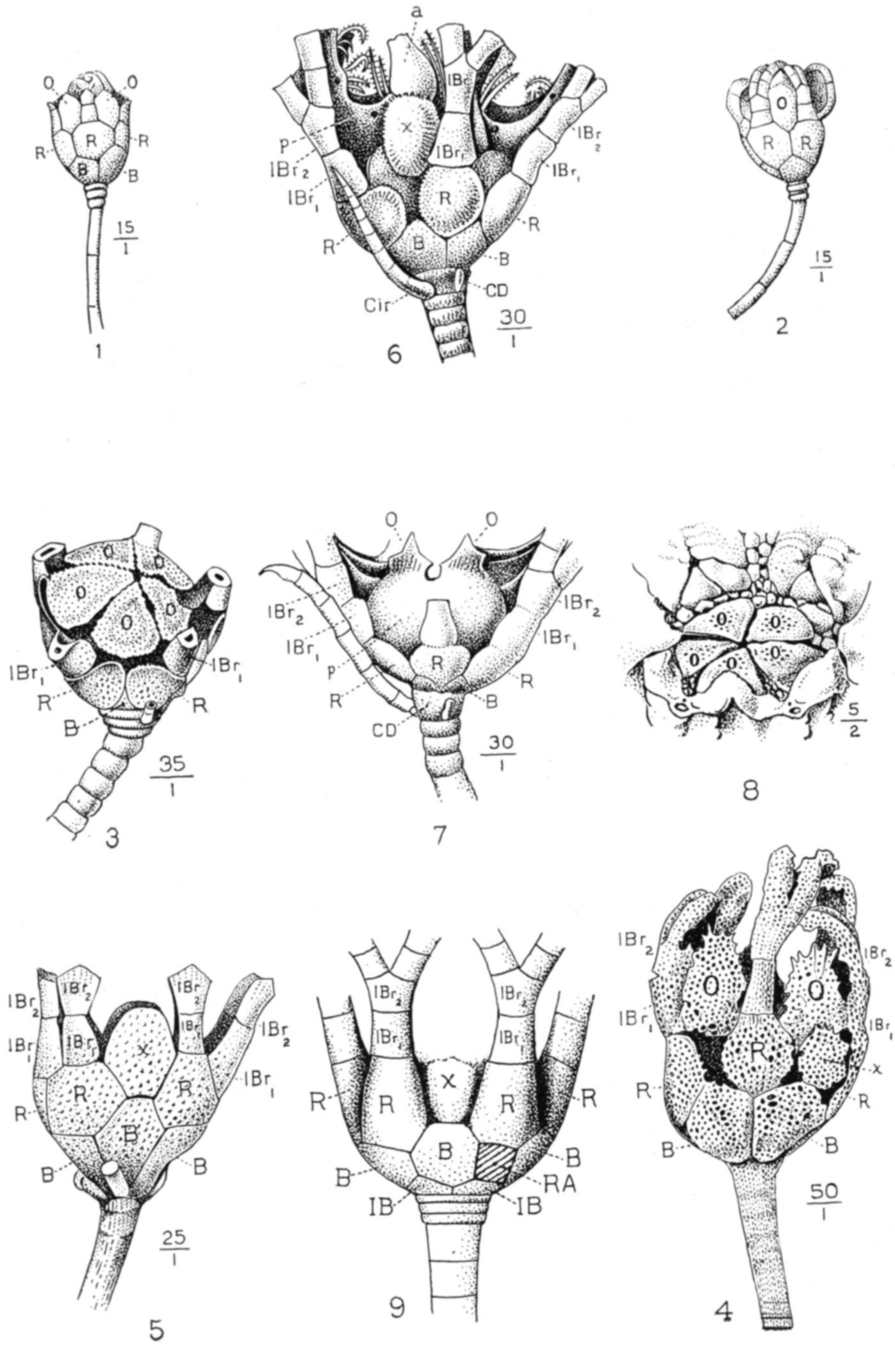
FIG. 1.—*C. fimbriatus* Ang. Upper Silurian, Gotland, Sweden. Anterior radial view; from original to Angelin, XXIX, 77.

FIG. 2—*Ibid.* Basal view of same specimen; the infrabasals covering the basals except at the posterior side, but partly removed at two places to show points of other basals.

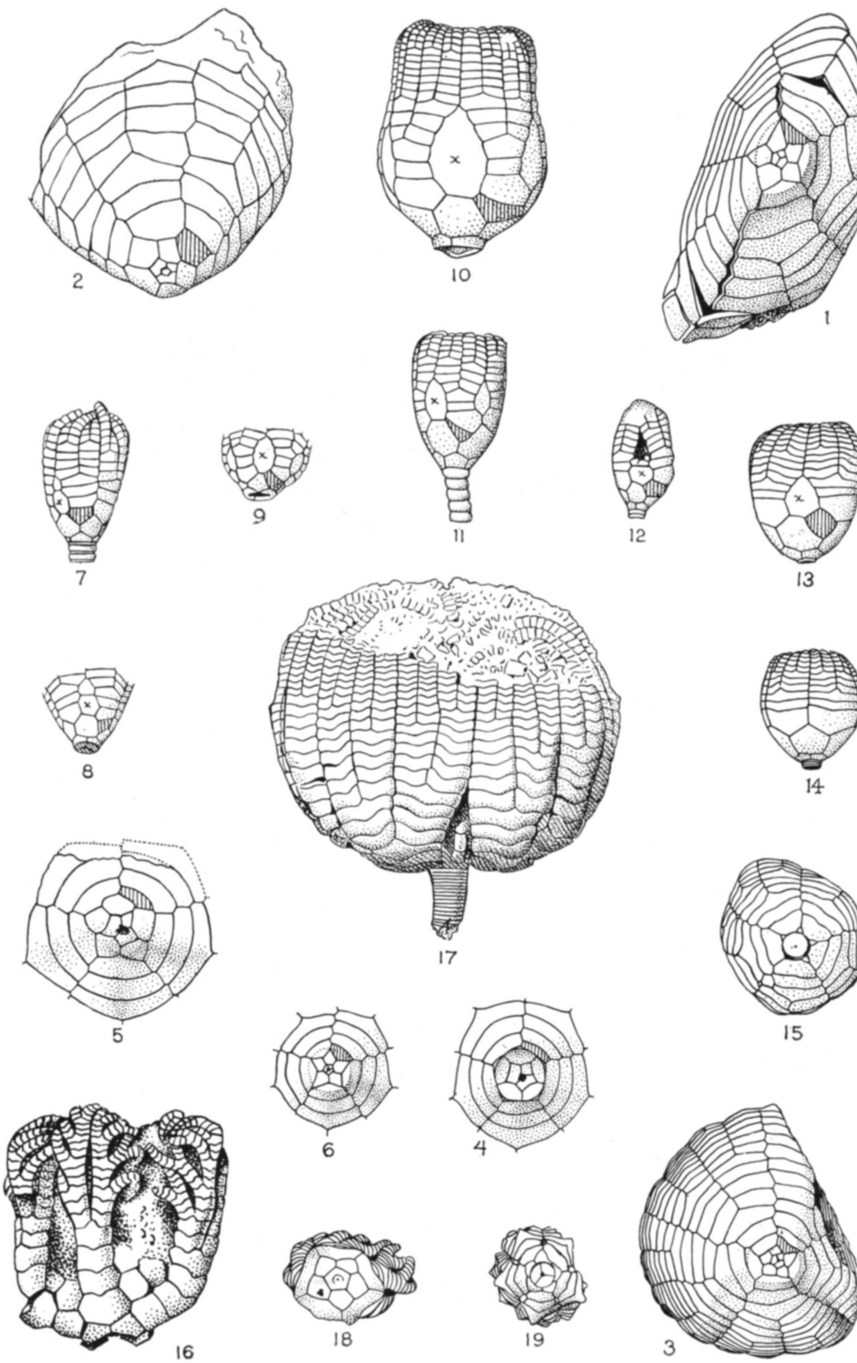
FIG. 3.—*C. heterodactylus* Ang. Upper Silurian, Gotland, Sweden. Basal view of calyx, with column ossicle attached; showing the enormous infrabasals, with posterior and two other basals visible as mere points.

FIG. 4.—*C. ovatus* Ang. Upper Silurian, Gotland, Sweden. Basal view of calyx, from original to Angelin, XVI, 17–19; all basals except the posterior completely hidden by the infrabasals.





K. M. Chapman, Del.



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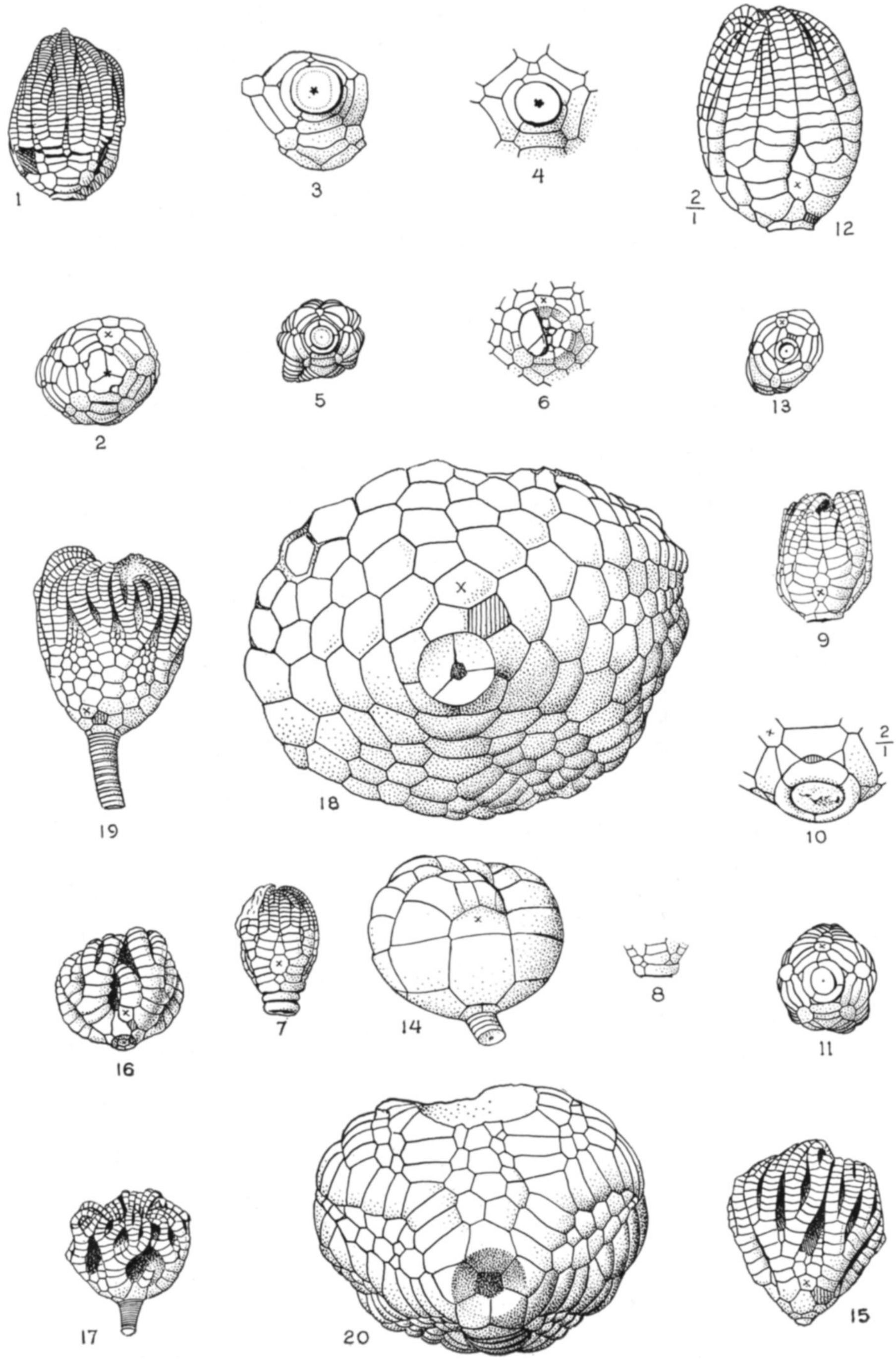

K. M. Chapman, Del.

FIG. 5.—*Ibid.* Basal view of another specimen, with column ossicle attached; no basal whatever visible.

FIG. 6.—*Ibid.* Basal view of another specimen; the infrabasals enveloping basals, radials, and part of first primibrachs. Part of the infrabasals have been removed, exposing the other plates beneath them, by which their relative positions and proportions can be seen.

FIG. 7.—*C. fimbriatus*, supra. Posterior view of crown with two column ossicles attached; from original to Angelin, XXIX, 77*b*.

FIG. 8.—*Ibid.* Left anterior radial view of base of same specimen; to show relative proportions of infrabasals and basals.

HOMALOCRINUS Angelin

FIG. 9.—*H. parabasalis* Ang. Upper Silurian, Gotland, Sweden. Posterior view of crown, from original to Angelin, XVI, 29; the very small radianal is visible, directly under the right posterior radial.

FIG. 10.—*Ibid.* Right posterior radial view of base of same specimen; showing radianal more distinctly. ×2.

FIG. 11.—*Ibid.* Basal view of same specimen, showing basals visible all around; radianal cannot be seen in this view. Nat.

FIG. 12.—*H. dudleyensis* n. sp. Upper Silurian. Dudley, England. Posterior view of crown, showing radianal directly under right posterior radial. ×2.

FIG. 13.—*Ibid.* Basal view of same specimen. Nat.

MESPILOCRINUS de Koninck and Lehon

FIG. 14.—*M. forbesianus* de Kon. and Leh. L. Carboniferous, Belgium. Posterior view; no radianal. (After de Kon. and Leh.)

TEMNOCRINUS Springer

FIG. 15.—*T. tuberculatus* Miller. Upper Silurian, Dudley, England. Posterior view of crown; radianal in primitive position as inferradial at base of right posterior ray.

GNORIMOCRINUS Wachsmuth and Springer

FIG. 16.—*Gn. expansus* Ang. Upper Silurian, Gotland, Sweden. Posterior view, from original to Angelin, XX, 16; anals in tubelike series; radianal obliquely under right posterior radial.

TAXOCRINUS Phillips

FIG. 17.—*T. shumardianus* Hall. Lower Carboniferous, Alabama. Posterior view; no radianal; anals in tubelike series, bordered by integument of small plates.

SAGENOCRINUS Austin

FIG. 18.—*S. expansus* Phill. Upper Silurian, Dudley, England. Basal view of a large specimen; radianal within the ring of basals and resting on the infrabasals; anal interredius perfectly filled with solid plates.

FIG 19.—*Ibid.* Right posterior view of smaller specimen.

FORBESIOCRINUS de Koninck and Lehon

FIG. 20.—*F. Washingtonensis* M. and G. L. Carboniferous, Indiana. Basal view of calyx; no radianal, and anal interradius perfectly filled with solid plates. The infrabasals are wanting in the specimen, having been detached with the stem, and fused with the proximal columnar.

(Figs. 1, 2, 7, 9, 10, 11, and 16 after Liljevall.)